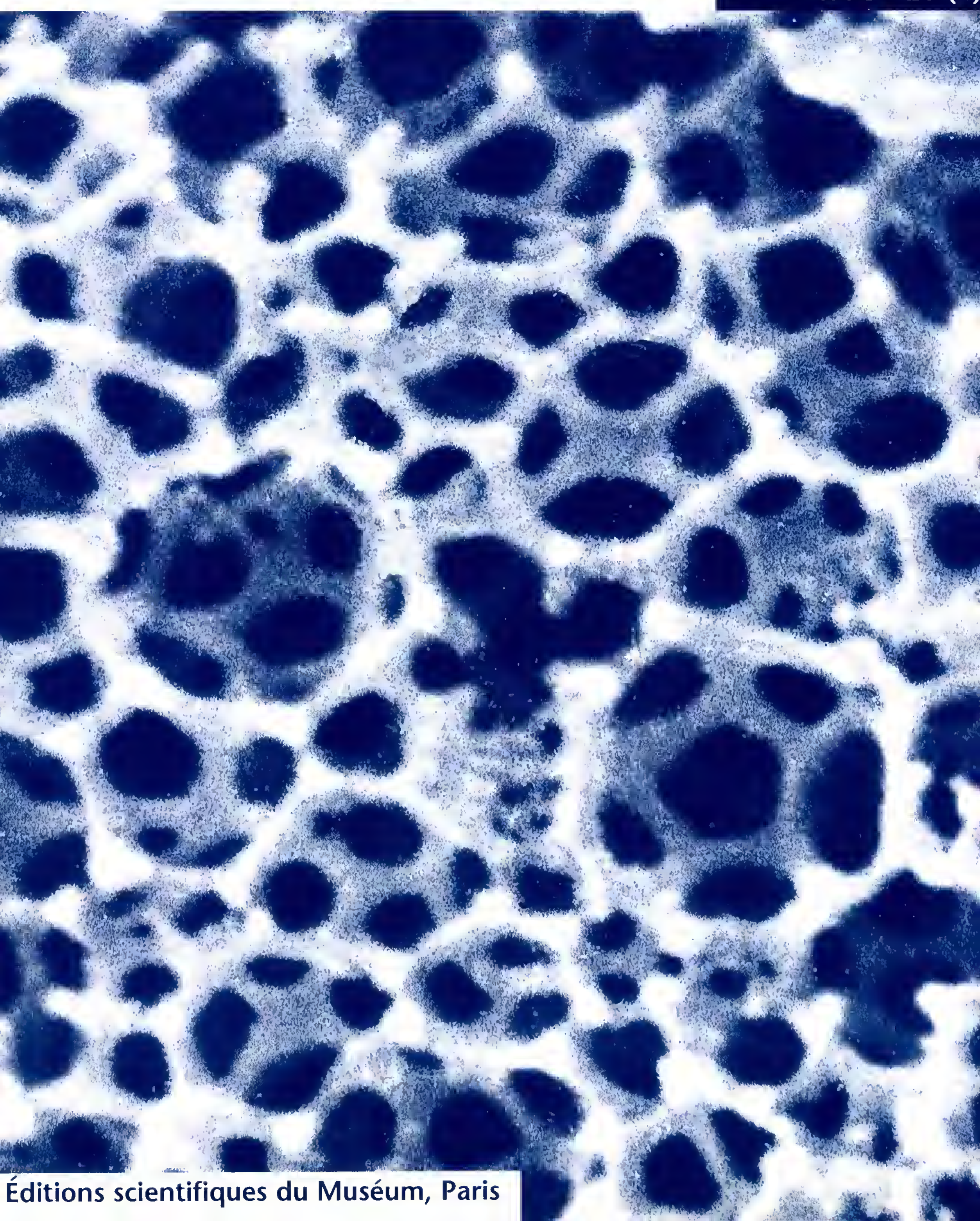
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Recent Brachiopoda from the oceanographic expedition SEAMOUNT 2 to the north-eastern Atlantic in 1993

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ABSTRACT
Eight species of recent brachiopods belonging to the genera *Neocrania, Dyscolia, Abyssothyris, Stenosarina, Eucalathis, Platidia, Phaneropora* and *Dallina* have been identified from collections from the 1993 SEAMOUNT 2 expedition to Meteor, Hyères, Irving-Cruiser, Plato, Atlantis, Tyro and Antialtair seamounts in the north-eastern Atlantic. The species misidentified by Jeffreys (1878) as *Terebratula vitrea* var. *sphenoidea* [*non* Philippi, 1844] is described as *Stenosarina davidsoni* n.sp. The affinities of the SEAMOUNT 2 brachiopods are with the Mauritanian biogeographic province. Diversity and number of stations yielding brachiopods increase from south to north in the cluster of six seamounts (Meteor-Tyro) south of the Azores. Brachiopod diversity for the seven seamounts as a whole is less than for the Canary Islands to the east. There is an as yet unexplained absence from the seamounts of deeper water species belonging to such genera as *Pelagodiscus, Hispanirhynchia, Terebratulina, Gryphus, Megerlia* and *Macandrevia*, which commonly occur around island archipelagos such as Madeira, the Canaries and the Cape Verdes, as well as off the Iberian coast and the African mainland.

KEY WORDS
Brachiopods,
Recent,
SEAMOUNT 2,
north-eastern Atlantic.

RÉSUMÉ

Brachiopodes actuels récoltés lors de l'expédition océanographique SEAMOUNT 2 dans l'océan Atlantique Nord-Est en 1993. Huit espèces de brachiopodes actuels appartenant aux genres *Neocrania, Dyscolia, Abyssothyris, Stenosarina, Eucalathis, Platidia, Phaneropora* et *Dallina* ont été identifiées à partir des collections réalisées lors de l'expédition SEAMOUNT 2 de 1993 aux pitons sous-marins Meteor, Hyères, Irving-Cruiser, Plato, Atlantis, Tyro et Antialtair dans l'océan Atlantique Nord-Est. L'espèce incorrectement identifiée par Jeffreys (1878) comme *Terebratula vitrea* var. *sphenoidea* [non Philippi, 1844] est décrite comme *Stenosarina davidsoni* n.sp. Les brachiopodes de SEAMOUNT 2 montrent une affinité avec la faune de la province biogéographique mauritanienne. La diversité et le nombre de stations où ces brachiopodes ont été observés augmentent du sud au nord dans le groupe des six pitons (Meteor-Tyro) au sud des Açores. La diversité en brachiopodes pour la totalité des sept pitons est inférieure à celle des îles Canaries à l'est. On observe sur ces pitons, sans pouvoir l'expliquer actuellement, une absence des espèces plus profondes appartenant aux genres *Pelagodiscus, Hispanirhynchia, Terebratulina, Gryphus, Megerlia* et *Macandrevia* qui se rencontrent normalement dans les archipels tels que Madère, les Canaries et les îles du Cap-Vert, ainsi que le long des côtes ibérique et africaine.

MOTS CLÉS
Brachiopoda,
actuel,
SEAMOUNT 2,
Atlantique Nord-Est.

INTRODUCTION

The SEAMOUNT 2 oceanographic expedition in 1993 to Meteor, Hyères, Irving-Cruiser, Plato, Atlantis, Tyro and Antialtair seamounts in the north-eastern Atlantic, west of Madeira and the Canary Islands and north and south of the Azores, sampled 165 stations (Gofas 1993). Of these, forty-eight stations (29%) yielded brachiopods. This proportion is comparable to those for brachiopods described from other Atlantic and Caribbean collections (Cooper 1977; Logan 1983, 1988) and confirms once again that they are not a common constituent of bottom samples except in high latitudes (Foster 1974). The location of all sampling stations is shown in Figure 1.

At the time of the study, the fifteen stations sampled off the western side of Grand Canary Island had not been sorted for brachiopods. Two out of forty-six stations (4%) on Meteor seamount yielded a total of three species, five out of twenty-four stations (21%) on Hyères seamount yielded a total of four species, thirteen out of thirty-five stations (37%) on Irving-Cruiser seamounts yielded four species, eight out of fourteen stations (57%) on Plato seamount yielded six species, fourteen out of twenty-one stations (67%) on Atlantis seamount yielded eight species, four out of six stations (67%) on Tyro seamount yielded five species and two out of four stations (50%) on Antialtair seamount yielded five species of brachiopods.

The following brachiopods have been recorded from the SEAMOUNT 2 Expedition and appear in the systematic section below:

Neocrania anomala (Müller, 1776);
Dyscolia wyvillei (Davidson, 1878);
Abyssothyris atlantica Cooper, 1977;
Stenosarina davidsoni n.sp.;
Eucalathis ergastica Fischer *et* Oehlert, 1890;
Platidia anomioides (Scacchi *et* Philippi, 1844);
Phaneropora incerta (Davidson, 1880);
Dallina septigera (Loven, 1846).

SYSTEMATICS

The supra-ordinal classification of Williams *et al.* (1996) has been used in this report, and, in accordance with usage in the forthcoming revised treatise on brachiopods; the terms "dorsal" and "ventral" are used for "brachial" and "pedicle" when describing the two valves. Since most species have been fully described elsewhere, only brief notes, illustrations of salient characteristics and a citation to a recent reliable description have been given here. Synonymies are therefore partial except for the newly-named species *Stenosarina davidsoni* Logan, which has been fully redescribed and illustrated. All types and figured specimens are deposited in the collections of the Muséum national d'Histoire naturelle (MNHN) in Paris, France. The exact location, depth and species identified at each station are shown in the Appendix.

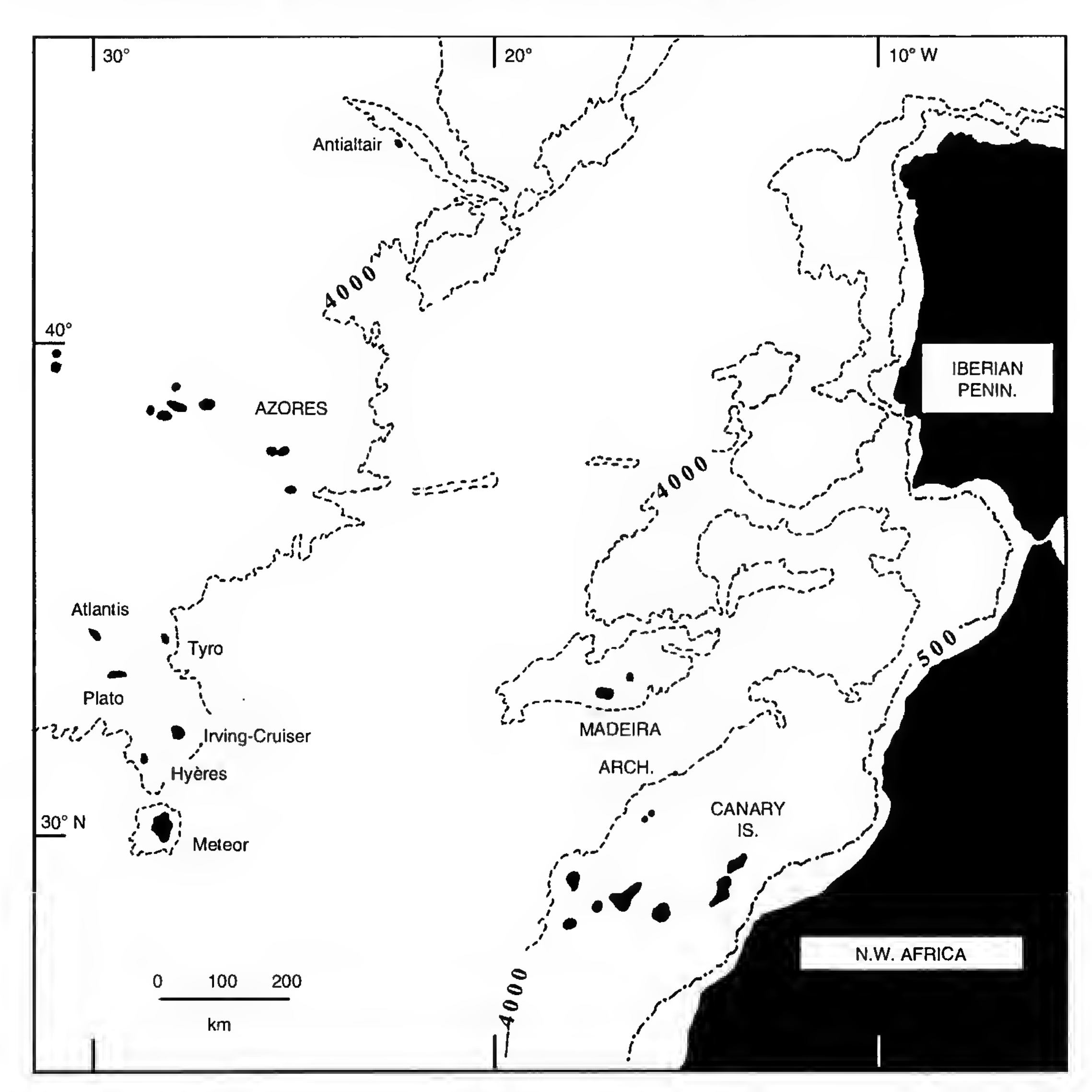


Fig. 1. — Map of the south-east North Atlantic to show the location of the seven seamounts from which brachiopods were obtained by the SEAMOUNT 2 expedition.

Sub-phylum CRANIIFORMEA
Popov, Bassett, Holmer *et* Laurie, 1993
Class CRANIATA Williams, Carlson, Brunton, Holmer *et* Popov, 1996
Order CRANIIDA Waagen, 1885
Suborder CRANIIDINA Waagen, 1885
Superfamily CRANIACEA Menke, 1828
Family CRANIIDAE Menke, 1828
Genus *Neocrania* Lee *et* Brunton, 1986

Neocrania anomala (Müller, 1776)
(Fig. 2A-C)

Crania anomala – Logan 1979: 27, figs 4, 5; pl. 1, figs 1-10.

STATIONS. — Irving-Cruiser: DW 215-216, DW 237; Plato: DW 240, DW 248; Atlantis: DW 254-257, DW 265, TS 270, DW 274; Tyro: 275, DW 277; Antialtair: DW 281, DW 283.

DEPTH RANGE. — 270-1665 m.

REMARKS
This species, one of the commonest brachiopods in the SEAMOUNT 2 collections, is a typical member of the brachiopod fauna of the eastern Atlantic (Fischer & Oehlert 1891; Brunton and Curry 1979; Anadon 1994), being found as far south as the Cape Verde Islands (Logan 1988) and ranging greatly in depth (Cooper 1981; this report). It is also common throughout the western Mediterranean, where it again ranges considerably in depth, although occurring most commonly in cryptic habitats in shallow water (Logan 1979; Logan & Noble 1983; Templado & Luque 1986). It is easily recognizable by its cone-shaped upper (dorsal) valve, subcircular outline, concentric growth lines and endopunctate shell, while internally the adductor muscle scars of both valves are arranged in pairs, posteriorly and anteriorly, on white callus pads, with a centrally-placed brachial protractor scar in the upper valve and a prominent median muscle scar in the very thin attached (ventral) valve. The shape of the shell, and particularly the attached valve, is variable, since it is strongly influenced by the irregularities of the substrate to which it is cemented (Fig. 2C). This substrate consists mainly of coarse sedimentary, volcanic or bioclastic material in the SEAMOUNT 2 collections. All specimens examined showed the typical dorsal valve internal characteristics of *N. anomala* rather than *N. turbinata* (Poli, 1795) which Brunton (1988) redescribed from the eastern Mediter-ranean.

Order TEREBRATULIDA Waagen, 1883
Suborder TEREBRATULIDINA Waagen, 1883
Superfamily TEREBRATULACEA Waagen, 1883
Family DYSCOLIIDAE Fischer *et* Oehlert, 1891
Genus *Dyscolia* Fischer *et* Oehlert, 1890

Dyscolia wyvillei (Davidson, 1878)
(Fig. 2D-F)

Dyscolia wyvillei – Cooper 1977: 56, pl. 15, figs 1-10.

STATIONS. — Meteor: DW 173; Hyères: DW 186, DW 203; Atlantis: DW 264.

DEPTH RANGE. — 795-1520 m.

REMARKS
This very large species occurs in the eastern Atlantic (Fischer & Oehlert 1891; Logan 1983; Saiz Salinas 1989) and the Caribbean (Cooper 1977) where the shells are usually collected in a very worn state. The loop of the brachial skeleton is rarely preserved in Recent specimens and the soft parts almost never, so the nature of the lophophore is uncertain, although one of Fischer & Oehlert's figures (1891, pl. 6, fig. 3i) suggests that it is trocholophous (see Cooper 1983 for further discussion). The specimens from SEAMOUNT 2 are all badly worn and show no brachial loops but the size and thickness of the shell, the large foramen and the distinctive fine radial ornamentation allow a positive identification to be made.

Family TEREBRATULIDAE Gray, 1840
Genus *Abyssothyris* Thomson, 1927

Abyssothyris atlantica Cooper, 1977
(Fig. 2G-M)

Abyssothyris atlantica Cooper, 1977: 58, pl. 20, figs 1-10.

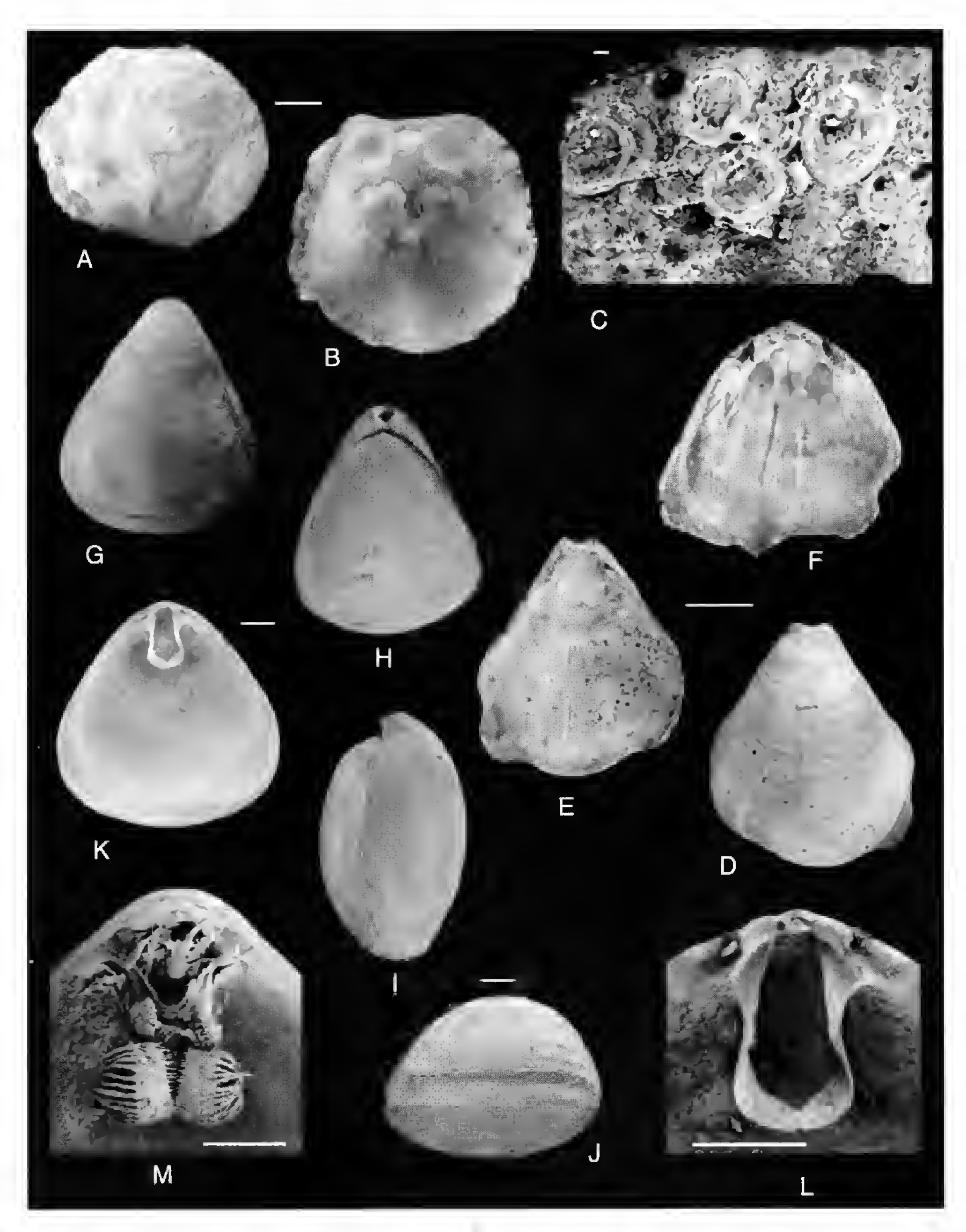


FIG. 2. — **A-C**, *Neocrania anomala* (Müller); **D-F**, *Dyscolia wyvillei* (Davidson); **G-M**, *Abyssothyris atlantica* Cooper. **A**, **B**, SEMs of exterior and interior of upper (dorsal) valve, the latter showing details of the muscle scars, DW 274, 280 m, Atlantis seamount, MNHN LBIMM-BRA-2781, 2782; **C**, fragment of volcanic rock with several attached lower (ventral) valves, DW 256, 340-345 m, Atlantis seamount, MNHN LBIMM-BRA-2783; **D-F**, ventral valve exterior showing fine radial ornamentation, ventral valve interior of same specimen showing worn hinge teeth and dorsal valve interior showing sockets and adductor scars, DW 173, Meteor seamount, 920 m, MNHN LBIMM-BRA-2784, 2785; **G-J**, SEM ventral, dorsal, side and anterior views to show external ornament and slightly sulcate anterior commissure, DW 279, Tyro seamount, 760-805 m, MNHN LBIMM-BRA-2786, 2787, 2788, 2789; **K**, SEM of dorsal valve interior to show loop of brachial skeleton, same locality and depth as previous specimen, **L**, enlargement of previous specimen, MNHN LBIMM-BRA-2790; **M**, SEM of dorsal valve interior with plectolophous lophophore covering loop of brachial skeleton, same locality and depth as previous specimen, MNHN LBIMM-BRA-2791. Scale bars: A, B, C, 1 mm; D-F, 1 cm; G-J, K, L, M, 1 mm.

STATIONS. — Meteor: DW 173; Plato: DW 241; Atlantis: DW 258; Tyro: DW 277-279.

DEPTH RANGE. — 420-1070 m.

REMARKS

This species was first described from over 2500 m depth, off Cape Fear, South Carolina, by Cooper (1977) who named it for very small elongate *Abyssothyris* with a broadly sulcate anterior margin. Specimens from SEAMOUNT 2 are less sulcate than the types but otherwise similar enough to the western Atlantic examples to be identified with them. The loop of *Abyssothyris* is rounded anteriorly with a slight median angularion. The plectolophous lophophore is small and tightly coiled (Fig. 2M) but lacks the median connecting band illustrated by Cooper (1983) for *A. elongata* and said to be typical of the genus. However, Cooper's illustrated specimen (*op. cit.*, pl. 16, fig. 19) came from depths of over 3600 m, whereas *A. atlantica* from SEAMOUNT 2 occurs at much shallower depths. Members of the genus typically occur in deep water and the development of the lophophore may be related to the effects of great depths, such as hydrostatic pressure and oxygen content (Zezina 1975). This is the first record of the genus from the eastern Atlantic.

Genus *Stenosarina* Cooper, 1977

Stenosarina davidsoni n.sp.
(Fig. 3A-J)

Terebratula vitrea var. *sphenoidea* [not Philippi, 1844] – Jeffreys 1878: 404, pl. 22, fig. 6?

Liothyris sphenoidea [*sensu* Jeffreys, 1878] – Davidson 1886: 12, pl. 2, figs 17, 18 only.

Terebratula (Liothyrina) sphenoidea [*sensu* Jeffreys, 1878] – Fischer & Oehlert 1891, p. 58, pl. 3, fig. 8a-m.

Liothyrina sphenoidea [*sensu* Jeffreys, 1878] – Blochmann 1908: 619, pl. 37, fig. 11; pl. 38, fig. 19a-c; pl. 39, fig. 23a-b.

Dallithyris? aff. *D.*? *sphenoidea* [*sensu* Jeffreys, 1878] – Cooper 1981: 15, pl. 2, figs 36-38.

Stenosarina sphenoidea [*sensu* Jeffreys, 1878] – Cooper 1983: 272, pl. 14, figs 15-19.

Stenosarina sphenoidea [*sensu* Jeffreys, 1878] – Logan 1988: 64.

MATERIAL EXAMINED. — Atlantis seamount, DW 258, holotype MNHN LBIMM-BRA-2778, paratypes MNHN LBIMM-BRA-2779, 2780.

STATIONS. — Hyères: DW 184, DW 186, DW 197, DW 203; Irving-Cruiser: DW 218-219, DW 225-227, DW 229, DW 231, DW 237-238; Plato: DW 241-242, DW 246-248, DW 251; Atlantis: DW 254-256, DW 258-259, DW 263, DW 265, DW 271; Tyro: DW 277-278; Antialtair: DW 283.

DEPTH RANGE. — 275-1715 m.

DESCRIPTION

Exterior

Shell white, thin and translucent, rarely exceeding 20 mm in length and 15 mm in width; elongate oval in outline, widest point just anterior to mid-valve, with anterior margin gently rounded. Both valves more or less evenly convex, with lateral commissure weakly concave towards ventral side near mid-valve; anterior margin rectimarginate. Beak suberecr, labiate; foramen moderate in size, permesothyridid.

Interior

Ventral valve interior with small, narrowly elongate teeth; short pedicle collar. Dorsal valve with narrow, parallel-sided loop which occupies about one third the length of the valve. Cardinal process small, socket ridges curved, flanking a socket roofed at its proximal end. Ourer hinge plates triangular and concave, extending anteriorly to join crural bases. Crura typical for the genus, as described and illustrated in detail by Cooper (1983: 271, 272).

REMARKS

This species, the commonest brachiopod in the SEAMOUNT 2 collections, has in the past been assigned to the genera *Terebratula*, *Liothyris*, *Liothyrina*, *Dallithyris*? and *Gryphus* by earlier authors, prior to *Stenosarina* by Cooper in 1983, under the specific epithet *sphenoidea*. Davidson (1886), Fischer & Oehlert (1891), Blochmann (1908), Dall (1920), Muir-Wood (1959), Cooper (1981, 1983) and Logan (1988) have all discussed the problems that have arisen from

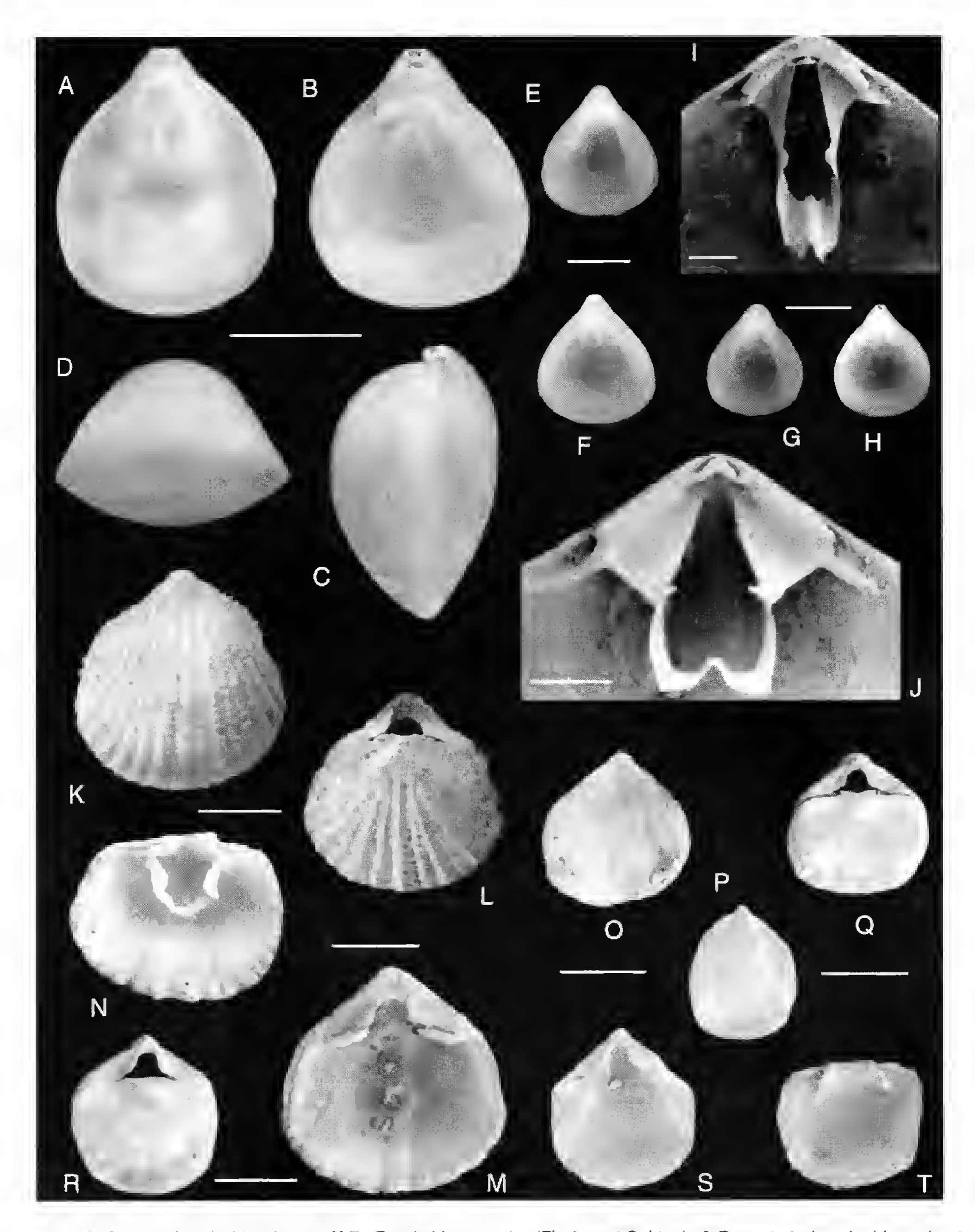


FIG. 3. — **A-J**, *Stenosarina davidsoni* n.sp.; **K-T**, *Eucalathis ergastica* (Fischer et Oehlert). **A-D**, ventral, dorsal, side and anterior views of holotype to show external ornament and rectimarginate anterior commissure, DW 258, Atlantis seamount, 420-460 m, MNHN LBIMM-BRA-2778; **E**, **F**, ventral and dorsal views of paratype 1, MNHN LBIMM-BRA-2779; **G**, **H**, ventral and dorsal views of paratype 2, same locality and depth as previous specimen, MNHN LBIMM-BRA-2780; **I**, **J**, SEM enlargements of loop of brachial skeleton of dorsal valve, straight and tilted, to show V-shaped notch in transverse band, same locality and depth as previous specimen, MNHN LBIMM-BRA-2792; **K**, **L**, SEMs of exterior of ventral and dorsal valves to show ornament, DW 264, Atlantis seamount, 795-830 m, MNHN LBIMM-BRA-2793, 2794; **M**, **N**, SEMs of interior of ventral and dorsal valves to show dentition and brachial skeleton, DW 283, Antialtair seamount, 1175-1210 m, MNHN LBIMM-BRA-2795, 2796; **O-T**, SEMs of exterior and interior of ventral and dorsal valves of juvenile specimens to show subdued ornament and rudimentary brachial skeleton, DW 274, Atlantis seamount, 280 m, MNHN LBIMM-BRA-2797 to 2802. Scale bars: A-D, E, F, G, H, 1 cm; I, J, K, L, M, N, O-T, 1 mm.

Jeffreys'misidentification of the eastern Atlantic Recenr form with Philippi's (1844) Pliocene species *Terebratula sphenoidea.* Dall (1920), Muir-Wood (1959) and Cooper (1981, 1983) have pointed out rhe main differences, which need not be repeated here, between rhe Pliocene and modern form. The above synonymy contains only those references where good descriptions and/or illustrations ensure identification with the modern form.

Several authors (Muir-Wood 1959; Cooper 1981) have called for the establishment of a new species name to avoid further confusion of modern and Pliocene forms. Jeffreys (1878) recognized two varieties of *Terebratula vitrea,* for which he used two names established by Philippi (1844): *minor* and *sphenoidea.* Neither is an appropriate designation for the modern eastern Atlantic form. A further complication is that Jeffreys'figure is faintly costellate, a condition that I have nor seen in typical eastern Atlantic *Stenosarina* and which Muir-Wood (1959) feels is represented erroneously. Enough material has been found in the present study to warrant a redescription of this species as a new taxon, which I here propose to call *Stenosarina davidsoni* in honour of the eminent brachiopod palaeontologist Thomas Davidson.

The species occurs in the eastern Atlantic as far south as rhe Canary and Cape Verde Islands (Logan 1988). Cooper (1981) is in error in stating that it occurs in the Mediterranean.

Family CANCELLOTHYRIDIDAE Thomson, 1926
Subfamily EUCALATHINAE Muir-Wood, 1965
Genus *Eucalathis* Fischer *et* Oehlert, 1890

Eucalathis ergastica Fischer *et* Oehlert, 1890
(Fig. 3K-T)

Eucalathis ergastica – Cooper 1981: 12, pl. 1, figs 1-8. – Logan 1983: 173.

STATIONS. — Meteor: DW 136; Hyères: DW 203; Plato: DW 249; Atlantis: DW 255, DW 258, DW 261, DW 264, TS 270, DW 274; Tyro: DW 278; Antialtair: DW 283.

DEPTH RANGE. — 280-1800 m.

REMARKS

Eucalathis ergastica and its closely related congener *E. tuberata* (Jeffreys), originally described from the south-east North Atlantic by Fischer & Oehlert (1891), are common brachiopods in the SEAMOUNT 2 and CANCAP collections (Logan 1983, 1988, this report). Cooper (1981) and Saiz Salinas (1989) have also recorded this species from the Bay of Biscay and Anadon (1994) from the coast of Asturias, northern Spain. The differences between the two species are mainly in their size, shape and ornament, *E. tuberata* being smaller and more rounded, with more numerous beaded radial costella. Juveniles of *E. ergastica* (Fig. 4E-J) have a more subdued ornament of less closely-spaced costellae than the adult forms. The species occurs off the Azores and the Canary Islands, the north coast of Spain and the Moroccan coast (Cooper 1981).

Suborder TEREBRATELLIDINA
Muir-Wood, 1955
Superfamily TEREBRATELLACEA King, 1850
Family PLATIDIIDAE Thomson, 1927
Genus *Platidia* Costa, 1852

Platidia anomioides (Scacchi *et* Philippi, 1844)
(Fig. 4A-D)

Platidia anomioides – Cooper 1977: 122, pl. 20, figs 11-19; pl. 33, figs 15-17. – Logan 1979: 60, figs 17, 18; pl. 7, figs 1-11.

STATIONS. — Irving-Cruiser: DW 209, DW 225; Plato: DW 242; Atlantis: DW 254-258, DW 262-265, TS 270, DW 274; Antialtair: DW 281.

DEPTH RANGE. — 275-1160 m.

REMARKS

This heavily-spiculate species is relatively common throughout the North Atlantic, particularly on its eastern side (Brunton & Curry 1979; Cooper 1981; Logan 1983; Saiz Salinas 1989; Anadon 1994). It also occurs in the Caribbean region (Cooper 1977) but is commonest in the Mediterranean (Logan 1979) where, as in the

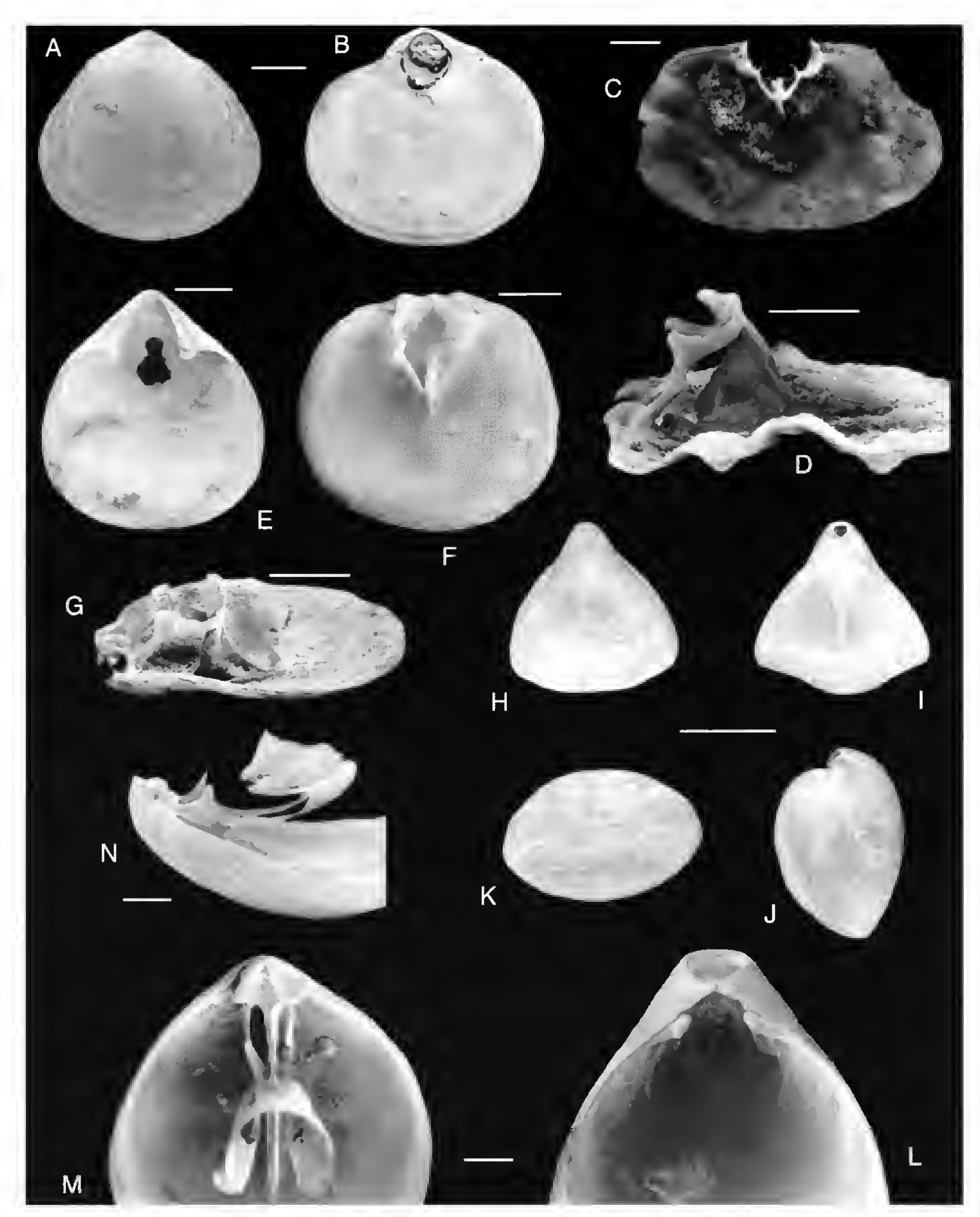


FIG. 4. — **A-D**, *Platidia anomioides* (Scacchi *et* Philippi); **E-G**, *Phaneropora incerta* (Davidson); **H-N**, *Dallina septigera* (Loven). **A**, **B**, SEMs of exterior of ventral and dorsal valves, to show convex ventral valve, flat dorsal valve, and amphithyridid pedicle foramen shered by both valves, DW 258 and 256, respectively, Atlantis seamount, 420-460 m and 340-345 m, MNHN LBIMM-BRA-2803, 2804; **C**, **D**, SEMs showing tilted dorsal and side views of interior of dorsal valve to show spicules and brachial support for lophophore, DW 264, Atlantis seamount, 795-830 m, MNHN LBIMM-BRA-2505; **E**, SEM of interior of ventral valve to show hinge teeth, DW 281, Atlantis seamount, 1190-1340 m, MNHN LBIMM-BRA-2806; **F**, **G**, SEMs of dorsal and side views of interior of dorsal valve to show sockets and brachial support for lophophore, same locality and depth as previous specimen, MNHN LBIMM-BRA-2807; **H-K**, ventral, dorsal, side and anterior views to show external ornament and sulcate anterior commissure, DW 241, Plato seamount, 695 m, MNHN LBIMM-BRA-2808, **L-N**, SEMs of ventral, dorsal and side dorsal views of two interiors to show teeth, sockets and brachial loop, DW 281, Antialtair seamount, 300 m, MNHN LBIMM-BRA-2809, 2810. Scale bars: A, B, C, D, 1 mm; E, F, G, 0.5 mm; H-K, 1 cm; L-N, 1 mm.

Atlantic, it is usually attached to bioclastic debris. Logan (1979) has shown that *P. anomioides* can be distinguished most reliably from its closely-related congener *P. davidsoni* (Deslongchamps) by slight differences in the configuration of the brachial skeleton. Removal of the lophophore of several SEAMOUNT 2 specimens to reveal this supporting structure has confirmed that they are indeed *P. anomioides.*

Family PHANEROPORIDAE Zezina, 1981
Genus *Phaneropora* Zezina, 1981

Phaneropora incerta (Davidson, 1880)
(Fig. 4E-G)

Phaneropora incerta – Logan 1983: 177, pl. 1, figs 11-17.

STATIONS. — Atlantis: DW 255, DW 261, TS 270.

DEPTH RANGE. — 335-1340 m.

REMARKS
This species was redescribed and illustrated from Madeira, the Canary and Cape Verde Islands by Logan (1983, 1988), who discussed the differences between the Atlantic species and the type species *P. galatheae* (Muir-Wood, 1965) from the Pacific. Davidson's species was questionably assigned to *Platidia* Costa by Fischer & Oehlert (1891) and, in fact, the internal skeletal characteristics of *Phaneropora* are not unlike those of *Platidia*, but externally the two genera are quite different in shape. Furthermore, the former genus lacks the large amphithyridid foramen shared by both valves, which results in a large hemispherical notch in each valve of *Platidia.*

Family DALLINIDAE Beecher, 1893
Genus *Dallina* Beecher, 1893

Dallina septigera (Loven, 1846)
(Fig. 4H-N)

Dallina septigera – Cooper 1981: 23, pl. 2, figs 41-43.

STATIONS. — Hyères: DW 200, DW 203; Irving-Cruiser: DW 219; Plato: DW 241-242, DW 248; Atlantis: DW 258, DW 263; Tyro: DW 277-279; Antialtair: DW 281, DW 283.

DEPTH RANGE. — 420-1210 m.

REMARKS
Dallina septigera is a common species throughout the north-eastern Atlantic and has been well described and illustrated by previous authors (Davidson 1886; Fischer & Oehlert 1891; Atkins 1960; d'Hondt 1976; Brunton & Curry 1977; Cooper 1981; Logan 1983, 1988; Anadon, 1994). It has a distinctive triangular outline, is widest anteriorly and has a sulcate anterior commissure. The brachial skeleton forms a long loop with a wide hood-like transverse ribbon (Fig. 4M, N).

DISCUSSION

The earliest expeditions to make extensive collections of brachiopods in the eastern Atlantic island archipelagos were those of the French research vessels *Travailleur* in 1882 and *Talisman* in 1883 (Fischer & Oehlert 1891). Since then six Dutch CANCAP expeditions to the same regions between 1976 and 1982 have significantly added to our knowledge of brachiopods from this region (Logan 1983, 1988, 1993), although there is still a dearth of information on brachiopods from the Azores. In terms of biogeographic affinities, the SEAMOUNT 2 brachiopods are typical of the Mauritanian faunal province. The affinities of the Mauritanian brachiopods to those from the Lusitanian and Mediterranean faunal provinces have been discussed by Logan (1993). No species new to science have been described in this study, although the genus *Abyssothyris* has been recorded for the first time from the eastern Atlantic, and the former species *Stenosarina sphenoidea* (Jeffreys) [not Philippi] has been renamed *Stenosarina davidsoni* n.sp.
There is a gradual increase in the number of stations yielding brachiopods, and the number of species identified, from south to north in the cluster of six seamounts (Meteor-Tyro) south of the Azores. Nevertheless, diversity for the whole seamount region is low, only eight species of bra-

chiopods being identified in this study, compared to sixteen species in the Canary-Salvage Islands area (Logan 1993). This relative paucity is not believed to be an artifact of the sampling and sorting efficiency of the collectors; rather it may be, at least partially, explained by the depths, sampling methods and bottom types of the stations sampled. Depths range from about 300 m to over 3000 m, with most over 500 m, so that predominantly shallow-water species belonging to the genera *Argyrotheca* Dall, 1900; *Megathiris* d'Orbigny, 1847, *Thecidellina* Thomson, 1915; *Pajaudina* Logan, 1988, and *Lacazella* Munier-Chalmas, 1881, which were commonly obtained by the earlier CANCAP expeditions at depths of less than 600 m (Logan 1983, 1988, 1993), were not encountered in SEAMOUNT 2 samples. More difficult to explain, however, is the absence from the seamounts of deeper water species belonging to genera such as *Pelagodiscus, Hispanirhynchia, Terebratulina, Gryphus, Megerlia* and *Macandrevia*, which commonly occur around island archipelagos such as Madeira, the Canaries and Cape Verde Islands, as well as off the Iberian coast and the African mainland (Fischer & Oehlert 1891; d'Hondt 1976; Logan 1983, 1988; Saiz Salinas 1989; Anadon 1994). Most SEAMOUNT 2 bottom samples were obtained by either dredge or epibenthic sled (Gofas pers. comm.), whereas the CANCAP samples were obtained mainly by Van Veen grab (Logan 1983). It is possible that some small and/or fragile brachiopod shells might have been lost or damaged by the sampling methods employed by SEAMOUNT 2.

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APPENDIX

STATION LIST

Station	Location	Depth	Species
METEOR			
DW 136	30°01'N - 28°28'W	305 m	*Eucalathis ergastica*
DW 173	30°03'N - 28°43'W	920-1070 m	*Dyscolia wyvillei*, *Abyssothyris atlantica*
HYÈRES			
DW 184	31°24'N - 28°52'W	675-705 m	*Stenosarina davidsoni*
DW 186	31°26'N - 28°51'W	1520 m	*Dyscolia wyvillei*, *Stenosarina davidsoni*
DW 197	31°18'N - 28°33'W	1370-1480 m	*Stenosarina davidsoni*
DW 200	31°19'N - 28°36'W	1060-1100 m	*Dallina septigera*
DW 203	31°09'N - 28°43'W	845 m	*Stenosarina davidsoni*, *Dallina septigera*, *Dyscolia wyvillei*, *Eucalathis ergastica*

Station	Location	Depth	Species
IRVING-CRUISER			
DW 209	31°59'N - 27°56'W	435-460 m	*Platidia anomioides*
DW 215	31°53'N - 28°02'W	270-275 m	*Neocrania anomala*
DW 216	31°53'N - 28°02'W	270 m	*Neocrania anomala*
DW 218	31°52'N - 28°53'W	420-480 m	*Stenosarina davidsoni*
DW 219	32°00'N - 27°53'W	760 m	*Dallina septigera*, *Stenosarina davidsoni*
DW 225	32°08'N - 28°10'W	1030-1035 m	*Platidia anomioides*, *Stenosarina davidsoni*, ? *Terebratulina* sp.
DW 226	32°06'N - 28°08'W	580 m	*Stenosarina davidsoni*
DW 227	32°07'N - 28°08'W	695-730 m	*Stenosarina davidsoni*
DW 229	32°02'N - 28°24'W	1715 m	*Stenosarina davidsoni*
DW 231	32°01'N - 27°54'W	745-750 m	*Stenosarina davidsoni*
TS 234	32°00'N - 27°41'W	1860-1880 m	? *Pelagodiscus* sp.
DW 237	32°16'N - 27°31'W	670-715 m	*Neocrania anomala*, *Stenosarina davidsoni*
DW 238	32°17'N - 27°32'W	890-900 m	*Stenosarina davidsoni*
PLATO			
DW 240	33°12'N - 29°01'W	565-575 m	*Neocrania anomala*
DW 241	33°11'N - 28°59'W	695 m	*Dallina septigera*, *Stenosarina davidsoni*, *Abyssothyris atlantica*
DW 242	33°11'N - 28°56'W	690-710 m	*Stenosarina davidsoni*, *Platidia anomioides*, *Dallina septigera*
DW 246	33°13'N - 29°36'W	520-550 m	*Stenosarina davidsoni*
DW 247	33°13'N - 29°35'W	580-625 m	*Stenosarina davidsoni*
DW 248	33°13'N - 29°32'W	670-735 m	*Dallina septigera*, *Stenosarina davidsoni*, *Neocrania anomala*
DW 249	33°12'N - 29°15'W	1700-1800 m	*Eucalathis* sp. cf. *ergastica*
DW 251	33°13'N - 29°28'W	900-985 m	*Stenosarina davidsoni*
ATLANTIS			
DW 254	34°05'N - 30°13'W	275-280 m	*Platidia anomioides*, *Neocrania anomala*, *Stenosarina davidsoni*
DW 255	34°05'N - 30°15'W	335-340 m	? *Eucalathis* sp., *Platidia anomioides*, *Neocrania anomala*, *Stenosarina davidsoni*, *Phaneropora incerta*
DW 256	34°06'N - 30°16'W	340-345 m	*Neocrania anomala*, *Platidia anomioides*, *Stenosarina davidsoni*
DW 257	34°04'N - 30°15'W	330-338 m	*Neocrania anomala*, *Platidia anomioides*
DW 258	33°59'N - 30°12'W	420-460 m	*Stenosarina davidsoni*, *Platidia anomioides*, *Dallina septigera*, ? *Eucalathis* sp., *Abyssothyris atlantica*
DW 259	33°59'N - 30°11'W	635-665 m	*Stenosarina davidsoni*
DW 261	34°22'N - 30°27'W	1190-1340 m	*Phaneropora incerta*, *Eucalathis ergastica*
DW 262	34°23'N - 30°29'W	1000-1160 m	*Platidia anomioides*

Station	Location	Depth	Species
DW 263	34°26'W - 30°32'W	610-655 m	*Dallina septigera*, *Platidia anomioides*, *Stenosarina davidsoni*
DW 264	34°24'N - 30°31'W	795-830 m	*Dyscolia wyvillei*, *Platidia anomioides*, *Eucalathis ergastica*
DW 265	34°28'N - 30°35'W	540-545 m	*Neocrania anomala*, *Stenosarina davidsoni*, *Platidia anomioides*
TS 270	34°04'N - 30°14'W	330 m	*Neocrania anomala*, ? *Eucalathis* sp., *Platidia anomioides*, ? *Phaneropora* sp.
DW 271	33°54'N - 30°09'W	1220 m	*Stenosarina davidsoni*
DW 274	34°05'N - 30°13'W	280 m	*Platidia anomioides*, *Neocrania anomala*, *Eucalathis ergastica*
TYRO			
DW 275	34°03'N - 28°18'W	1590-1665 m	*Neocrania anomala*
DW 277	33°59'N - 28°20'W	945-1000 m	*Neocrania anomala*, *Abyssothyris atlantica*, *Stenosarina davidsoni*, *Dallina septigera*
DW 278	33°57'N - 28°22'W	890-925 m	*Dallina septigera*, *Stenosarina davidsoni*, *Eucalathis ergastica*, *Abyssothyris atlantica*
DW 279	33°55'N - 28°23'W	760-805 m	*Dallina septigera*, *Abyssothyris atlantica*
ANTIALTAIR			
DW 281	43°34'N - 22°25'W	900 m	*Dallina septigera*, *Platidia anomioides*, *Neocrania anomala*
DW 283	43°34'N - 22°19'W	1175-1210 m	*Stenosarina davidsoni*, *Dallina septigera*, *Neocrania anomala*, *Eucalathis ergastica*

The *Paracyclops fimbriatus*-complex (Copepoda, Cyclopoida): a revision

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ABSTRACT
The type species of *Paracyclops*, *P. fimbriatus* (Fischer, 1853), is redescribed based on material from the vicinity of St Petersburg in Russia, one of the type localities. The taxonomic status of *P. fimbriatus*, *P. chiltoni* (Thomson, 1882) and *P. imminuta* Kiefer, 1929 are stabilised and a neotype is designated for *P. fimbriatus*. It is revealed that failure to separate *P. imminuta* from the other two species of the complex was the main factor responsible for the taxonomic confusion concerning all three. Characters traditionally used by taxonomists, such as proportional measurements of the caudal rami and the terminal spines of the third endopodal segment of leg 4 are found to vary considerably within populations as well as between populations. Since there is extensive overlap in variability expressed between these three variable species, it is therefore concluded that most early records are unreliable. Previously overlooked characters which can help to differentiate between them are introduced, including the ornamentation of the frontal surface of the coxobasis of antenna, of the posterior surface of leg 1, and of the caudal rami.

KEY WORDS
Copepoda,
P. fimbriatus,
P. imminuta,
P. chiltoni,
taxonomy,
Palaearctic.

RÉSUMÉ
Le complexe Paracyclops fimbriatus *(Copepoda, Cyclopoida) : une révision.* L'espèce-type de *Paracyclops, P. fimbriatus* (Fischer, 1853) est redécrite à partir de matériel collecté à St Pétersbourg en Russie, une localité-type. Le statut systématique de *P. fimbriatus*, de *P. chiltoni* (Thomson, 1882) et *P. imminuta* Kiefer, 1929 est redéfini et un néotype est désigné pour *P. fimbriatus*. Il apparaît que la difficulté de séparer *P. imminuta* des deux autres espèces est la raison principale de la confusion systématique régnant dans ce complexe d'espèces. Les caractères utilisés jusqu'à présent, en particulier les mesures relatives des branches furcales et des épines terminales du troisième segment de l'endopodite de P4 présentent des variations considérables pour une population donnée et également entre populations et se recouvrent en partie chez les trois espèces. Cette variabilité extrême ne permet pas de les séparer clairement, les données anciennes paraissant parfois incertaines. D'autres caractères pouvant aider à différencier les trois espèces sont introduits comme l'ornementation de la face frontale du coxobasis de l'antenne, de la face postérieure de P1 (basipodite et coxopodite), des rames furcales et la structure du réceptacle séminal de la femelle.

MOTS CLÉS
Copepoda,
P. fimbriatus,
P. imminuta,
P. chiltoni,
taxonomie,
Paléarctique.

INTRODUCTION

The earliest record assigned to *Paracyclops fimbriatus* (Fischer, 1853) by Dussart & Defaye (1985) is that of the Danish naturalist O. F. Müller who described it under the name *Cyclops crassicornis* Müller, 1785. Müller's (1785) description and illustrations were based on an early copepodid stage and are grossly inadequate, so that it is almost impossible to determine whether he was dealing with a cyclopoid or harpacticoid. The type material of *Cyclops crassicornis* cannot be traced and probably is no longer extant. If *C. crassicornis* is a cyclopoid it can be best considered as *species incertae sedis* in the family Cyclopidae. Unfortunately Sars (1863) identified some of his specimens as *C. crassicornis* although he expressed some reservations about conspecificity with Müller's material. In spite of this uncertainty *C. crassicornis* became established in the literature since other workers (Uljanin 1875; Brady 1878; Herrick 1882) followed Sars and ignored or overlooked Fischer's (1853) important paper on the cyclopids from St Petersburg. It was not until 1892 that Brady (1892) recognized Fischer's (1853) *Cyclops fimbriatus* and discarded Müller's *C. crassicornis* as a valid species of cyclopid. Sars (1913-1918) independently arrived at the same conclusion and regarded it as very questionable that *Cyclops crassicornis* belongs to the genus *Cyclops*.

The origins of the current taxonomic confusion surrounding the genus *Paracyclops* in general, and the so-called *P. fimbriatus* complex in particular, are threefold.

Firstly, Fischer's (1853) original description of the type species *P. fimbriatus*, full and valid by contemporary mid-nineteenth century standards but inadequate by modern standards, has been accepted as the standard reference and consequently has led to problems in later taxonomic work. It is therefore not surprising that the species has been reported from a wide range of freshwater habitats all over the world.

A second factor that has contributed significantly to the taxonomic confusion is the publication of various incompletely described species or forms that are closely related to the type-species and can

be considered as forming part of a *P. fimbriatus* species complex: these include *P. chiltoni* (Thomson, 1882), *P. finitimus* Kiefer, 1928, *P. abnobensis* Kiefer, 1929 and *P. fimbriatus* forma *imminuta* Kiefer, 1929.

Finally, in the course of this study it became apparent that the traditional means of differentiating species within the genus *Paracyclops*, such as the morphology of the caudal rami and leg 5, are insufficient and in some cases completely misleading since virtually no account has been taken of intra- or inter-population variation.

Recent progress in copepod systematics has raised the level of taxonomic resolution of these freshwater copepods and it has been demonstrated several times that many cyclopoid species, reported earlier as cosmopolitan in freshwater habitats, have a restricted geographical distribution (Kiefer 1981; Van de Velde 1984; Reid 1998). A similar situation has been demonstrated for the Cladocera (Frey 1980, 1982) and the Rotifera (Dumont 1983).

Prior to this revision, the geographical records and major synonyms of *P. fimbriatus* and *P. chiltoni* were summarized by Dussart & Defaye (1985) and indicated cosmopolitan distributions for both. So, it became vital to describe typical *P. fimbriatus* in detail. Attempts were made to locate the type material but Fischer's material is, in all probability, no longer extant. Unfortunately, Fischer did not designate a single type locality. Fischer's (1853) original paper was entitled "Contribution to the knowledge of Cyclopoids from the area of St Petersburg" and in this paper, it was stated that the *P. fimbriatus* material was collected from Madeira island, the vicinity of Baden-Baden (Germany), Iwanofskoje and Peterhof (around St Petersburg). There was no clear indication on which material his original description was based.

An attempt was made to collect *Paracyclops* material from the vicinity of St Petersburg. No *Paracyclops* material was found in the Peterhof pond but abundant *Paracyclops* material was collected from other localities in the vicinity of St Petersburg. The redescription given here is based on a neotype selected from this material, and supplemented by examination of numerous other collections from the Palaearctic region.

Examination of four unsorted samples from the vicinity of St Petersburg revealed four *Paracyclops* species: *P. fimbriatus*, *P. chiltoni*, *P. imminuta* and *P. poppei*. *Paracyclops poppei* can easily be separated from the other three species, but *P. fimbriatus*, *P. chiltoni* and *P. imminuta* are easily confused. Traditional means of differentiating between these taxa, such as the morphology of the caudal rami, the proportional length of terminal spines of leg 4 and the structure of leg 5 are insufficient and in some cases misleading, therefore most early records are unreliable.

The object of this paper is to redescribe *P. fimbriatus*, *P. imminuta* and *P. chiltoni* in detail, to identify their major synonyms and to introduce previously overlooked characters which are important in differentiating them.

METHODS

Specimens were dissected and mounted in lactophenol. Broken glass-fibres were added to prevent the appendages from being compressed by the coverslip and to facilitate rotation and manipulation which allowed viewing from all sides. All drawings were made with the aid of a camera lucida using an Olympus BH-2 microscope equipped with Nomarski differential interference contrast and all measurements made with an ocular micrometer. Body lengths were measured from the base of the rostrum to the posterior edge of the caudal rami. Body width is given as the widest part of the cephalothorax. In the spine and seta formula of the swimming legs Roman numerals and Arabic numerals are used for spines and setae, respectively. The terminology proposed by Huys & Boxshall (1991) is adopted. The terms "frontal" and "caudal" introduced by Van de Velde (1984) to denote the anterior and posterior surface of the antennary coxobasis are also adopted.

Abbreviations

NHM — The Natural History Museum, London;
MNHM — Muséum national d'Histoire naturelle, Paris;
ZM — Zoologisk Museum, Oslo;
USNM — United States National Museum, Smithsonian Institution, Washington.

SYSTEMATICS

Paracyclops fimbriatus (Fischer, 1853)
(Figs 1-9)

Original description:
Cyclops fimbriatus Fischer, 1853 [*Bull. Soc. Imp. Nat. Moscou* 26, 1: 94, figs 19-28, 30].

Synonymy:
Cyclops fimbriatus Fischer, 1853: 94, pl. III, figs 19-28, 30.

Cyclops crassicornis O. F. Müller, 1785 *sensu* Brady 1878: 118, 119, pl. 23, figs 1-6.

Cyclops soli Kokubo, 1912: 102, pl. II, figs 24-26.

Platycyclops fimbriatus (Fischer, 1853) – Sars 1913-1918: 81, 82, pl. L.

Cyclops (*Paracyclops*) *fimbriatus* Fischer, 1853 – Pesta 1928: 114-116, figs 96A-D, 97A-C. – Reuter-Schiltz & Hoffmann 1970: 229-231, figs 27-31.

Paracyclops fimbriatus f. *typica* (Fischer, 1853) – Kiefer 1929: 50, Abb. 53.

Paracyclops abnobensis Kiefer, 1929: 51, Abb. 57-59.

Paracyclops vagus Lindberg, 1939: 45-50, figs 1a-l.

TYPE MATERIAL. — A neotype is designated herein and deposited in the collection of the NHM, Reg. No. 1997.1762. It is a female collected at P. Dudergofka, St Petersburg, Russia and dissected on 4 slides.

OTHER MATERIAL. — **Russia.** River Igora (Neva system), about 10-15 km east of St Petersburg, depth 0.5 m, t 18 °C, 22.VII.1996, coll. V. Alekseev: 14 ♀♀. — P. Dudergofka, St Petersburg, 27.VII.1996, depth 0.5 m, t 18 °C, coll. V. Alekseev: 4 ♀♀. — River Ravan (Ladoya system), about 100 km east of St Petersburg, depth 0.2-0.5 m, t 17 °C, 22.VII.1996, coll. V. Alekseev: 2 ♀♀. — St Petersburg, water supply system, pond JWS, July 1984, coll. V. Alekseev: 1 ♂. — Baikal pulp & paper mill, pond of cleaning system, in the vicinity of Lake Baikal, 9.VII.1984, coll. V. Alekseev: 4 ♀♀, 3 ♂♂.
Turkey. Demirköprü, coll. Ü. Demirhindi: 7 ♀♀ (NHM 1966.3.24.23).
Sweden. Lake Malar, Upland: 4 ♀♀ (Norman Collection, NHM 1911.11.8.40935-939).
Ireland. Locality unspecified: 24 ♀♀, 7 ♂♂ (Norman Collection, 1911.11.8.40915-934; selected from more than 200 specimens in mixed sample, mostly *P. imminuta*). — Rossmore, Co. Monaghan: 1 ♀ (NHM 1911.11.8.40914).
Palestine. 33 ♀♀ (NHM 1938.3.9.83-89 1002a).
Norway. 69 ♀♀, 16 ♂♂ (G. O. Sars Collection ZM, F20478; no locality is given by G. O. Sars on the original label but on a second label is written "Norv" which indicates that the material is probably from Norway. This material contains a mixture of *P. fimbriatus* and *P. imminuta*.)
Mongolia. Lake Orog Nuur, Goby Desert, 11.VII. 1995, coll. V. Alekseev: 1 ♀, 14 ♂♂.
India. Nagarjuna University reservoir fed from River Krishna, 4.VIII.1976, coll. Y. Ranga Reddy: 7 ♀♀, 6 ♂♂. — River Krishna at Vijayawada, 16°31'N - 80°39'E, January 1974: 3 ♀♀.
Finland. Province of South Häme, municipality of Lammi, Lake Pääjärvi, western arm, organic ooze mixed with mineral particles at 3-5 m depth, 61°04'N - 25°08'E, 18.XI.1996, coll. J. Sarvala: 25 ♀♀, 1 ♂.
Germany. Oldenburg, 2.VIII.1996, coll. T. Ishida: 26 ♀♀, 12 ♂♂.
Japan. Tomakomai, Hokkaido, 4.XI.1987: 4 ♀♀, 8 ♂♂. — Same locality, 12.V.1987: 6 ♀♀, 1 ♂. — Ryuku, 12.V.1996, coll. T. Ishida: 1 ♀, 1 ♂. — Lake Biwa, Honshu, 17-18.III.1986, coll. T. Ishida: 2 ♀♀ dissected on two slides. — Hokkaido University, Sapporo, Hokkaido, 9.VIII.1987, coll. T. Ishida: 6 ♀♀ whole mounts on 1 slide, 2 ♂♂ whole mounts on 1 slide, 2 ♀♀ dissected on slide. — Tokachi, Hokkaido, 5.VIII.1983, coll. T. Ishida: 1 ♀, 1 ♂ whole mounts.
Uzbekistan. Town Muynak near Aral Sea, Kashkadavya Region, Chauvak Reservoir, Tashkent Region, coll. I. M. Mirabdullayev: 6 ♀♀.
Scotland. Loch Ness, 19.VII.1992: 7 ♀♀, 5 ♂♂.

DISTRIBUTION. — Examination of numerous collections of *Paracyclops* from the Palaearctic, Nearctic regions, and from Africa has revealed that *P. fimbriatus* is not as widely distributed as previously believed (Karaytug 1998). Based on examined materials, *P. fimbriatus* is, at present, known to be distributed in Europe and Asia extending eastwards to include Turkey, Palestine, China, Japan and India. *P. fimbriatus* appears to be widely distributed throughout the Palaearctic region.

REDESCRIPTION
Adult female
Body length and width not including caudal setae given in Table 1. Prosome (Fig. 1C) with cephalothorax narrowing anteriorly and three free pedigerous somites decreasing in width from anterior to posterior. Third pedigerous somite with minutely denticulate hyaline frill along the posterior margin. Third and fourth pedigerous somites with patch of spinules at each posterolateral corner. Urosome (Fig. 2A, B)

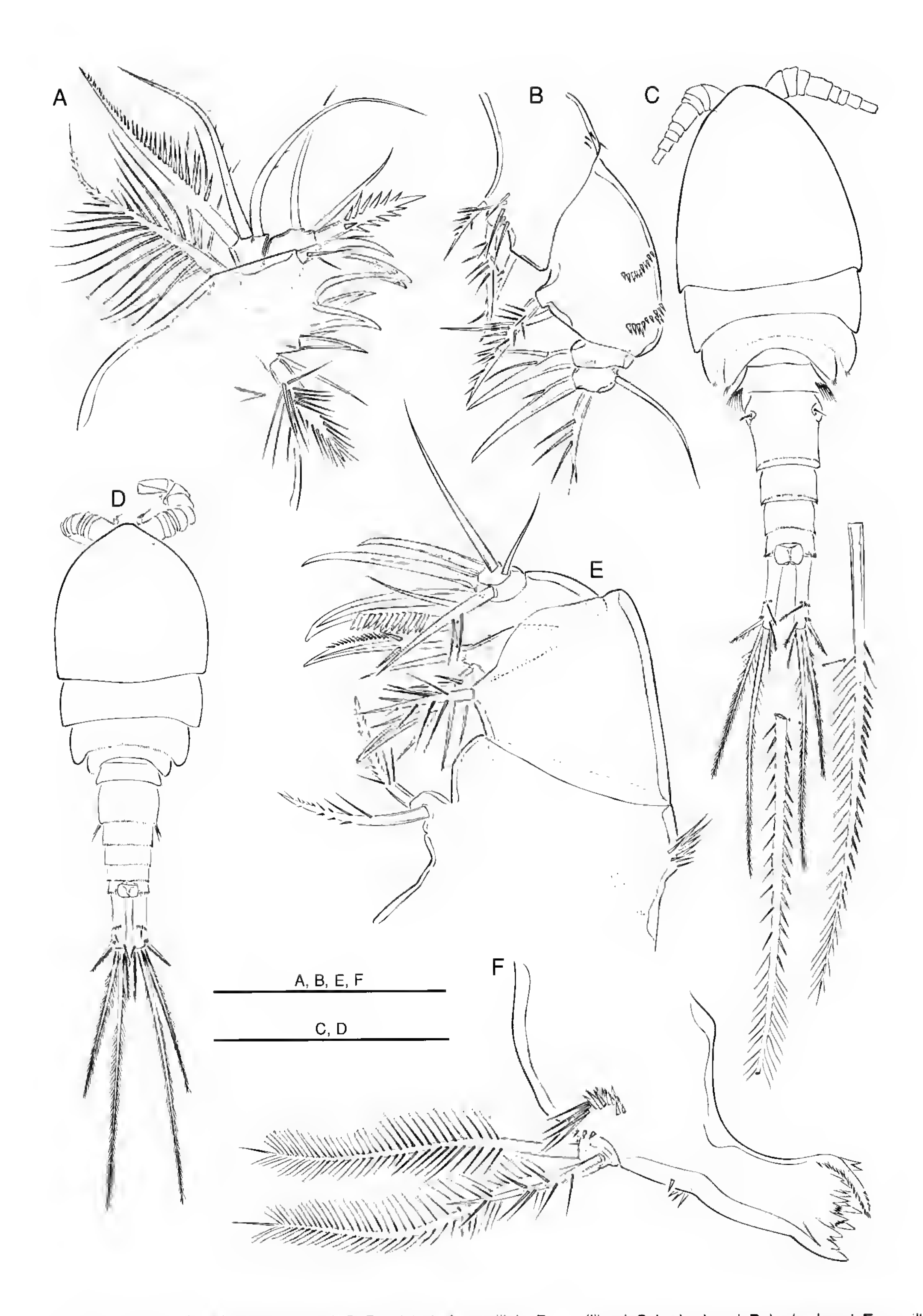


FIG. 1. — *P. fimbriatus*; **A-C**, **E**, **F**, neotype, adult ♀; **D**, adult ♂; **A**, maxillule; **B**, maxilliped; **C**, body, dorsal; **D**, body, dorsal; **E**, maxilla; **F**, mandible. Scale bars: A, B, E, F, 50 µm; C, D, 400 µm.

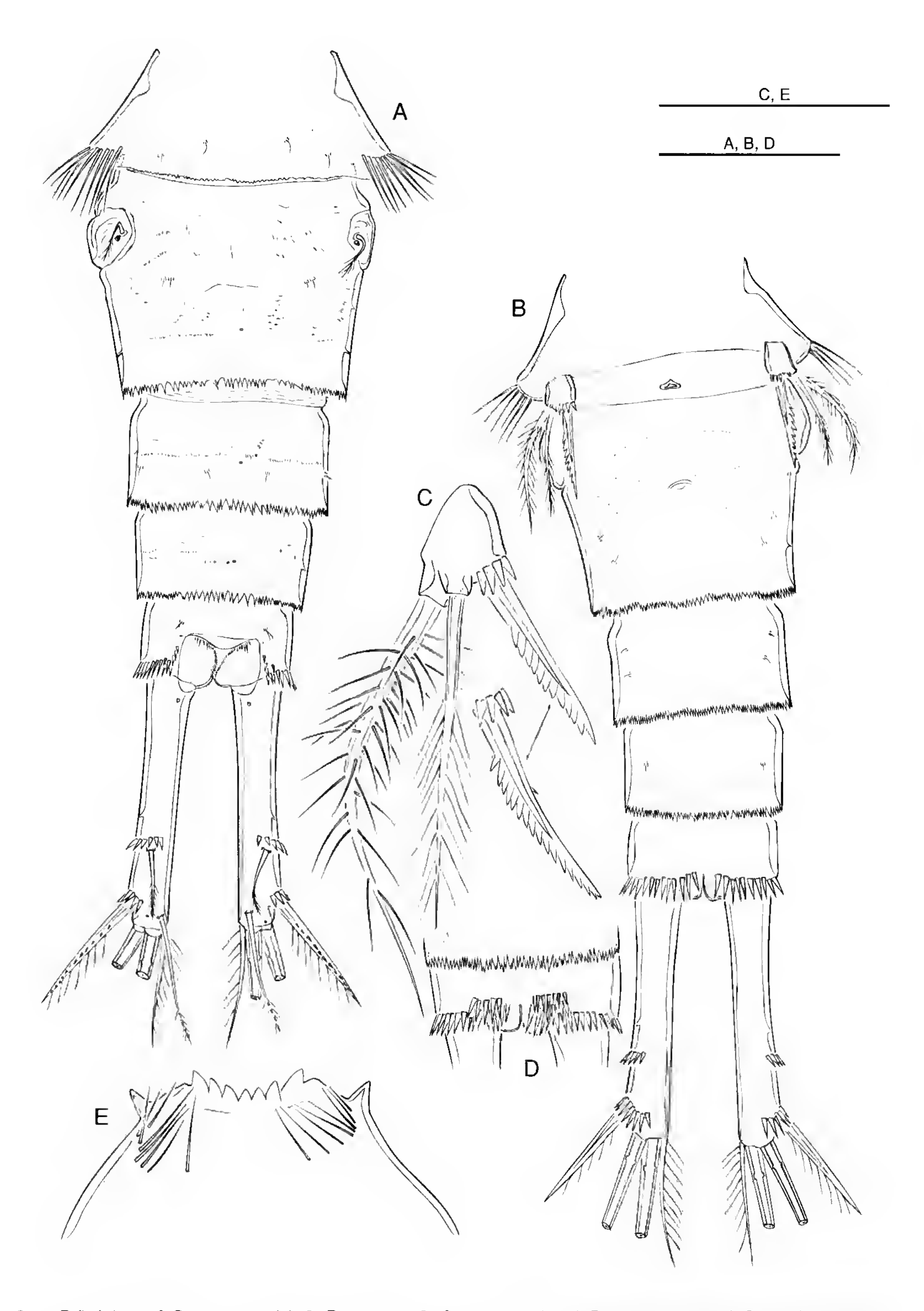


FIG. 2. — *P. fimbriatus*; **A-C**, neotype, adult ♀; **D**, non-type ♀; **A**, urosome, dorsal; **B**, urosome, ventral; **C**, leg 5, ventral; **D**, anal somite, ventral (St Petersburg); **E**, labrum. Scale bars: A, B, D, 100 μm; C, E, 50 μm.

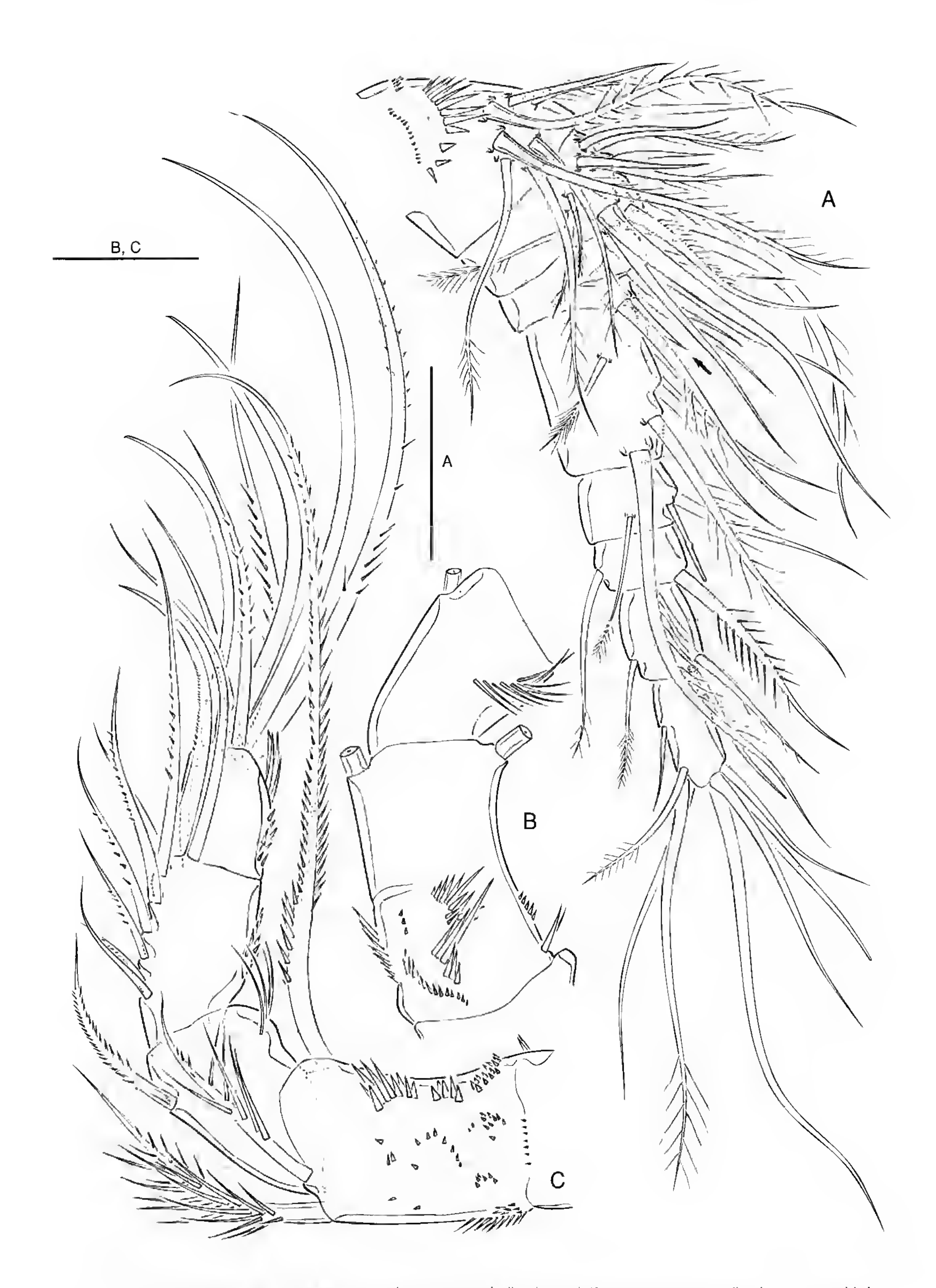


Fig. 3. — *P. fimbriatus*; neotype, adult ♀; **A**, antennule with arrow indicating spiniform seta at anterodistal corner on third segment; **B**, antenna, coxobasis and first endopodal segment, frontal; **C**, antenna, caudal. Scale bars: A, 50 µm; B, C, 25 µm.

consisting of fifth pedigerous somite, genital double-somite and three free abdominal somites. Fifth pedigerous somite with fringe-like elongate setules at posterolateral angles. Genital double-somite, second and third abdominal somites ornamented with irregular pattern of fine pits dorsally as figured (Fig. 2A). Seminal receptacle divided into broad anterior and posterior lobes (Fig. 2B). Median copulatory pore located ventrally about halfway along length of genital double-somite. Posterior margin of genital double-somite and following two abdominal somites with finely incised hyaline frill. Anal somite with ventral spinular row extending laterally and dorsally almost to either side of anal operculum. Anal operculum weakly developed, smooth; and opening bordered by spinular row (Fig. 2A).

Caudal rami with slightly convex inner margin; very variable in length and shape (Figs 2A, B, 7A-F); armed with six setae (Fig. 2A); seta (I) absent; anterolateral seta (II) plumose with spinules at base on dorsolateral surface; posterolateral seta (III) unilaterally plumose with spinules along dorsal surface, spinular row at base ventrally extending dorsally; terminal accessory seta (VI) plumose; outer terminal seta (IV) and inner terminal seta (V) well-developed and heterogeneously ornamented (Fig. 1C).

Antennule 8-segmented (Fig. 3A). First segment with ventral spinular rows in proximal half. Segment 3 with partial suture line and spiniform seta near anterodistal corner (arrowed in Fig. 3A). Segment 5 with characteristic short aesthetasc. Segment 7 with aesthetasc located distally on anteroventral margin. Apical segment with aesthetasc fused basally to adjacent seta. Setal formula 8, 12, 6, 5, 2 + 1 aesthetasc, 2, 2 + aesthetasc, 7 + aesthetasc.

Antenna 4-segmented (Fig. 3C), comprising coxobasis and 3-segmented endopod. Coxobasis with complex ornamentation on caudal (Fig. 3C) and frontal (Fig. 3B) surfaces as figured, and armed with two inner spinulose setae plus very long outer spinulose seta representing exopod. First endopodal segment with inner distal spinulose seta and spinules along outer margin. Second endopodal segment with nine setae, of which six along inner margin and three arranged around distal inner corner; ornamented with spinules along outer margin. Third endopodal segment armed with seven setae around apex; outer margin ornamented with short spinules proximally and long spinules distally.

Labrum (Fig. 2E) forming broad posterior outgrowth. Distal margin with strong teeth; anterior surface ornamented with paired groups of long spinules.

Mandible (Fig. 1F) consisting of well-developed coxal gnathobase and reduced palp. Gnathobasis blades pointed, mostly simple, dorsal seta with spinules along inner rim. Palp represented by minute segment, bearing three spinulose setae, two of which very long and one short. Coxa with spinular row along outer margin between palp and gnathobase, and with lateral group of spinules near insertion of palp.

Maxillule (Fig. 1A) consisting of powerful praecoxa and reduced 2-segmented palp. Praecoxal arthrite armed with six setae articulating at base and five spines fused to segment; proximalmost articulating spine spinulose, other spines naked. Proximal segment of palp representing fused coxa and basis, bearing one strong spine and two naked setae apically, plus outer spinulose seta representing exopod. Distal segment of palp, representing endopod, armed with three setae, outermost seta spinulose.

Maxilla 5-segmented (Fig. 1E) comprising praecoxa, coxa, basis and 2-segmented endopod. Praecoxa with spinular rows on outer margin and dorsally. Praecoxal endite with two spinulose setae. Coxa with proximal endite represented by single spinulose seta; distal endite cylindrical, with strong spinulose spine and naked seta apically. Basis drawn out into powerful curved claw bearing coarse spinules along middle part of inner margin; accessory armature consisting of strong spine; with spinular row along convex margin and naked seta. First endopodal segment carrying two setae, second with three setae.

Maxilliped 4-segmented (Fig. 1B) comprising syncoxa, basis, and 2-segmented endopod. Syncoxa armed with three spinulose setae representing endites, few long spinules arranged near base of setae; ornamented with spinular row near outer distal angle. Basis armed with one spinulose and one naked seta; ornamented with

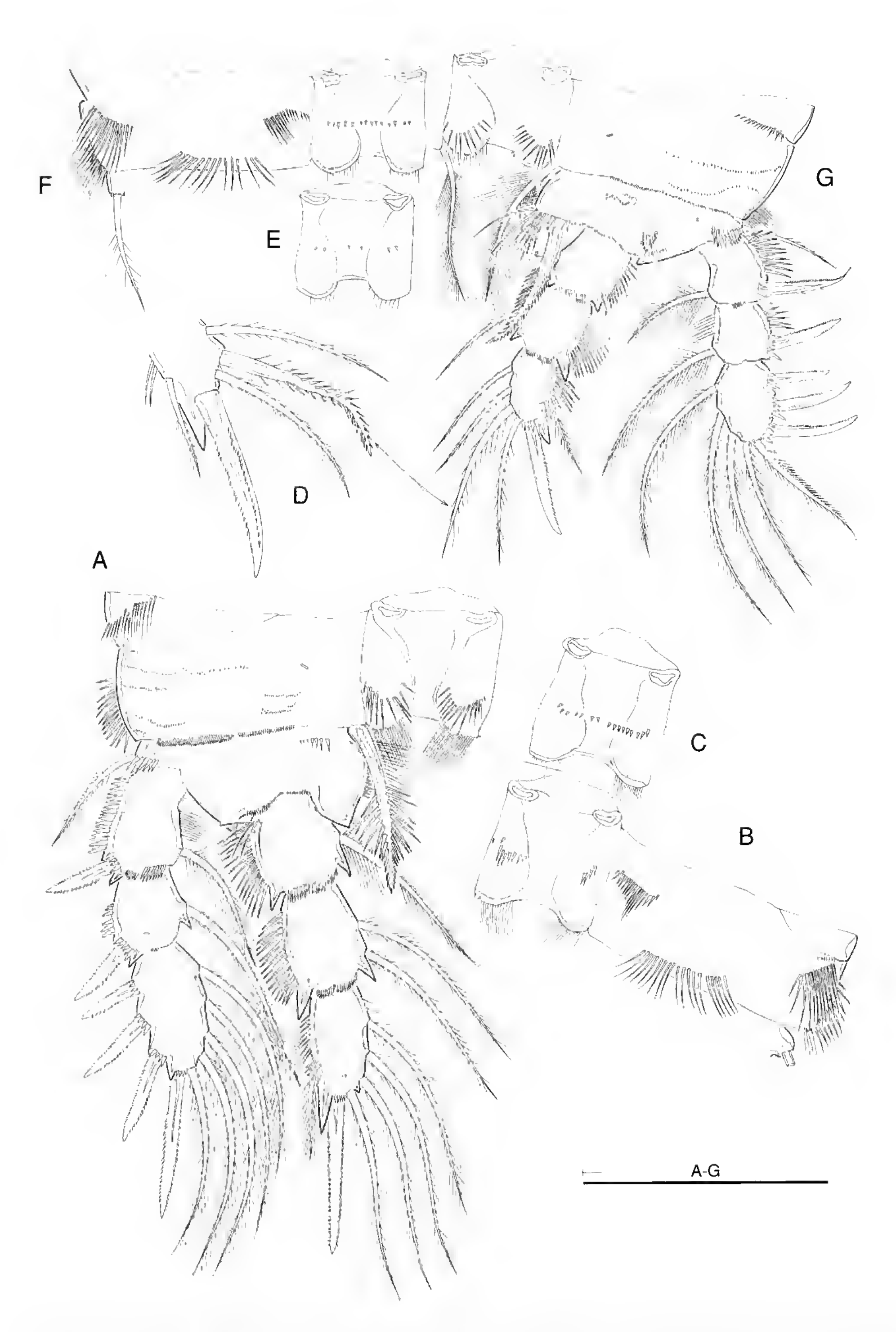


Fig. 4. — *P. fimbriatus*; **A**, **B**, **E**, **G**, neotype, adult ♀; **C**, non-type adult ♀; **D**, adult ♂; **F**, non-type ♀; **A**, leg 2, anterior; **B**, **C**, intercoxal sclerite and coxa of leg 2, posterior; **D**, terminal endopodal segment of leg 1; **E**, **F**, intercoxal sclerite and coxa of leg 1, posterior; **G**, leg 1, anterior view. Scale bar: 100 µm.

two transverse rows of spinules near outer margin. First endopodal segment bearing claw-like seta with spinules at midlength. Second endopodal segment with three setae, one of which naked; other spinulose.

Legs 1 to 4 with 3-segmented protopod (Figs 4A, G, 5A, F). Praecoxa represented by triangular sclerite at outer proximal angle; each protopodal segment with spinular row on outer corner of margin. Coxa with complex ornamentation on both anterior and posterior surfaces as figured. Basis with plumose outer seta. Endopodal segments with long spinules along outer margins. All spines on segments of both rami with spinules at their bases. Exopodal segments 1 and 2 with short spinules along outer margins. Legs 2 to 4 each with spinular rows on anterior surface of endopodal segments 1 and 2 and exopodal segment 1 and posteriorly on exopodal segments 1 and 2. Legs 2 and 3 with posterior spinular rows on endopodal segment 2.

Leg 1 (Fig. 4G): coxa with inner plumose seta. Basis with spinulose spine on inner margin bearing two groups of spinular rows at base, one of which long and fringe-like; also ornamented with spinular rows anteriorly near base of endopod. Intercoxal sclerite ornamented with spinular rows anteriorly (Fig. 4G) and posteriorly (Fig. 4E, F). Exopodal segments 1 and 2 and endopodal segment 2 with spinular rows posteriorly. Spine of exopodal segment 1 with flagellate apex. Seta next to outermost spine of terminal exopodal segment semispinulose (Fig. 4G).

Leg 2 (Fig. 4A): intercoxal sclerite with spinular rows anteriorly and posteriorly (Fig. 4A-C). Coxa with inner spinulose spine.

Leg 3 (Fig. 5F): intercoxal sclerite with (Fig. 5G) or without (Fig. 5F) spinular row anteriorly, with two spinular rows posteriorly (Fig. 5H). Coxa with inner spinulose spine.

Leg 4 (Fig. 5A): intercoxal sclerite with patch of spinules on anterior surface (Fig. 5A) and with three spinular rows posteriorly (Fig. 5B, C). Inner coxal spine with group of setules mainly originating posteriorly (Fig. 5C). Basis with spinular row near inner margin posteriorly (Fig. 5B, C). Endopodal segment 2 without spinular row posteriorly.

Spine and seta formula as follows:

	Coxa	Basis	Exopod	Endopod
Leg 1	0-1	1-I	I-1; I-1; III, 5	0-1; 0-1; 1, I, 4
Leg 2	0-I	1-0	I-1; I-1; III, I, 5	0-1; 0-2; 1, I, 4
Leg 3	0-I	1-0	I-1; I-1; III, I, 5	0-1; 0-2; 1, I, 4
Leg 4	0-I	1-0	I-1; I-1; II, I, 5	0-1; 0-2; 1, II, 2

Leg 5 (Fig. 2C) comprising single free segment, armed with one long (almost twice as long as inner spine) multispinulose outer seta, one strong inner spine with 3-4 spinules around base, and one plumose seta in middle. Leg 6 (Fig. 2A) represented by one plumose seta and one tiny spinule dorsolaterally.

Adult male

Body length 716 μm and width 260 μm (St Petersburg), the body length and width measurements of the males from other localities are given in Table 1. Body (Fig. 1D) differing from adult female as follows: urosome 6-segmented (Fig. 8A, C), comprising fifth pedigerous, genital and four free abdominal somites; genital, third, fourth and fifth urosomites ornamented with cuticular pits dorsally (also present ventrally on fourth urosomite). Caudal rami shorter than female.

Antennule digeniculate (Fig. 9A, C, D), indistinctly 15-segmented. Segment 1 armed with eight setae; one seta (seta A) large and modified by ornamentation of strong spinules in proximal and mid sections, tapering to fine point distally (see inset in Fig. 9D); ornamented with row of spinules ventrally (Fig. 9E). Segment 2 with four setae. Segment 3 with two setae. Segment 4 with two setae plus aesthetasc. Segments 5 and six each with two setae. Segments 7 and 8 separated from each other by extensive arthrodial membrane (Fig. 9D): segment 7 with two setae, segment 8 with two setae. Segment 9 with two setae plus a short aesthetasc, fused to segment 8. Segment 10 (= ancestral segment XV) produced on one side into sheath enclosing segment 11 ventrally; armed with two setae, one ornamented with long setules unilaterally, other longer and naked. Segment 11 bearing curved seta ornamented with

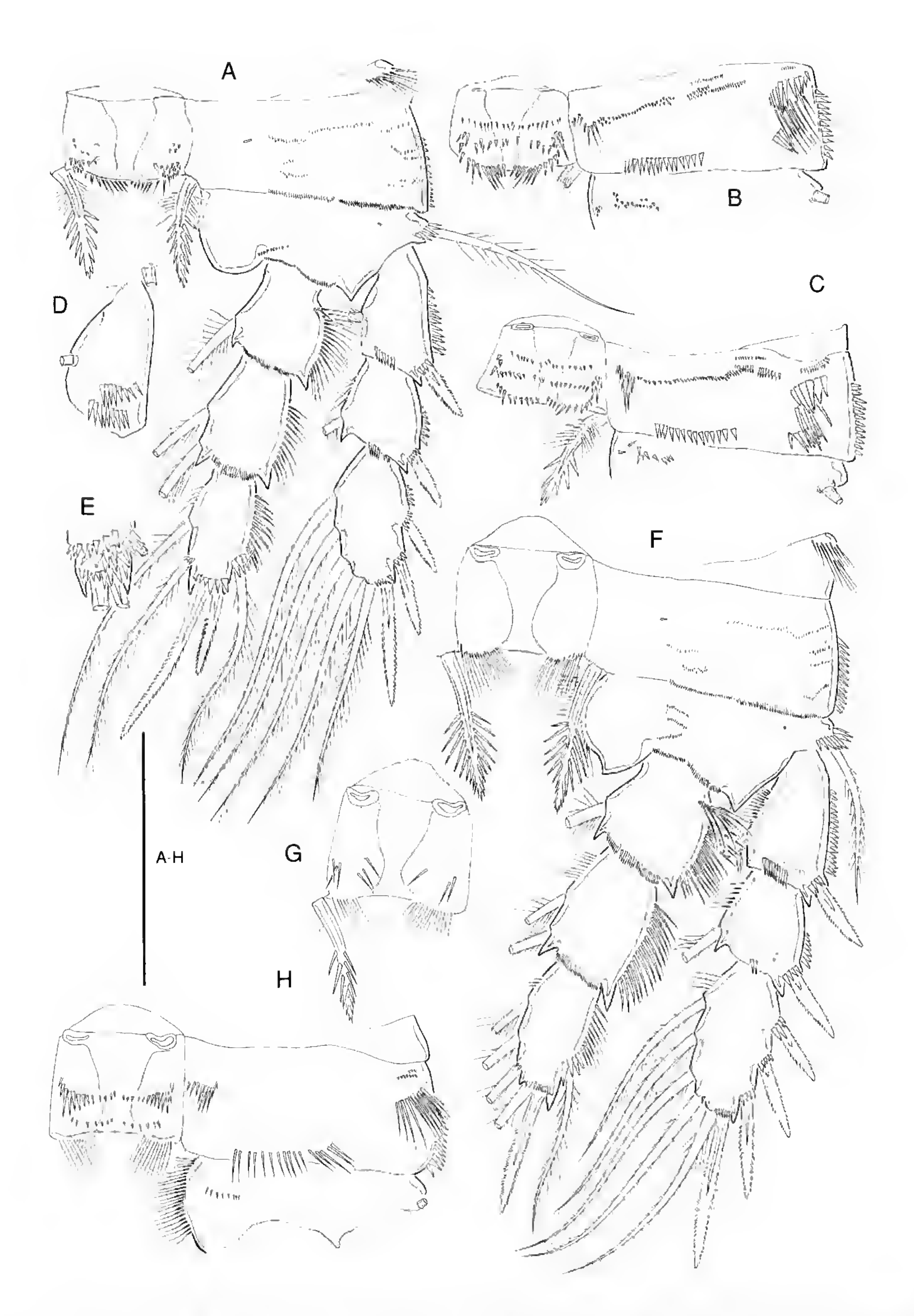


Fig. 5. — *P. fimbriatus*; **A**, **B**, **F**, neotype, adult ♀; **C**, **D**, **E**, non-type ♀; **A**, leg 4, anterior; **B**, **C**, intercoxal sclerite and coxa of leg 4, posterior; **D**, first exopodal segment of leg 4, posterior (Finland); **E**, terminal endopodal segment of leg 4, anterior; **F**, leg 3, anterior; **G**, intercoxal sclerite of leg 3, anterior; **H**, intercoxal sclerite and coxa of leg 3, posterior. Scale bar: 100 µm.

TABLE 1. — Body length (BL) and width (BW) measurements (in µm) of adult *Paracyclops fimbriatus* from various localities (N, number of specimens measured).

LOCALITY	SEX	BL (mean ± SD)	RANGE	BW (mean ± SD)	RANGE	N
St Petersburg (River Igora)	♀	885 ± 92.5	684-1017	309 ± 12.6	289-333	14
St Petersburg (P. Dudergofka)	♀	916 ± 91.5	815-993	370 ± 12.5	358-383	3
Russia (Vicinity of Lake Baikal)	♀	862 ± 52	802-894	314 ± 7.5	306-321	3
	♂	754 ± 16	738-770	254 ± 5	249-259	3
Mongolia	♀	743		296		1
	♂	651 ± 19.3	605-672	228 ± 15.4	202-249	10
India	♀	624 ± 22.9	600-662	231 ± 6.5	222-240	6
	♂	558 ± 27	527-589	204 ± 3.5	200-207	5
Turkey	♀	776 ± 67.5	707-854	302 ± 15.3	289-326	5
Finland	♀	893 ± 48.4	808-983	329 ± 9.3	313-351	12
	♂	786		262		1
Sweden	♀	923 ± 30.4	901-944	340 ± 27.6	320-359	2
Germany	♀	834 ± 38.2	786-926	336 ± 13.1	318-359	12
	♂	696 ± 31.6	641-728	280 ± 4.5	272-285	7
Japan	♀	862 ± 41.6	777-909	308 ± 13.6	282-328	9
	♂	748 ± 42.4	693-810	259 ± 4.9	247-268	9
Ireland	♀	831 ± 40.9	767-901	336 ± 16.2	311-363	10
	♂	721 ± 22.3	699-757	276 ± 7	268-285	5
Scotland	♀	916 ± 50.9	827-998	337 ± 21.5	295-359	7
	♂	816 ± 80.3	722-913	287 ± 18.7	264-307	5
Palestine	♀	743 ± 48.1	709-777	256 ± 2.8	254-258	2
Uzbekistan	♀	782 ± 32.5	724-846	258 ± 19	234-284	6

double row of strong denticles, plus one naked seta (Fig. 9A, C). Segment 12 armed with minute naked seta, plus short, highly chitinized spine. Segment 13 armed with one short spinulate seta proximally, four short naked setae, plus one modified element attached to segment by short stalk (Fig. 9A); main part of modified element lying along surface of segment and ornamented with longitudinal ridges and small central pore. Geniculation located between segments 13 and 14. Segments 14 and 15 partly fused (Fig. 9B), forming curved subchela-like section: segment 14 armed with two setae and two modified elements each ornamented with longitudinal ridges and a central pore (as proximal element on segment 13). Apical segment tapering distally; armed with eleven setae and one aesthetasc, mostly originating on outer (= posterior) surface. Segmental fusion pattern as follows: I-V, VI-VII, VIII, IX, X, XI, XII, XIII, XIV, XV, XVI, XVII, XVIII-XX, XXI-XXIII, XXIV-XXVIII.

All other appendages as in female except: coxobasis of antenna with additional spinular row near inner spinulose setae (arrowed in Fig. 8E), innermost seta of coxobasis strongly spinulated. One inner seta on endopodal segment 3 of leg 1 spinulose (Fig. 4D). Outer seta of fifth leg plumose and less developed than in

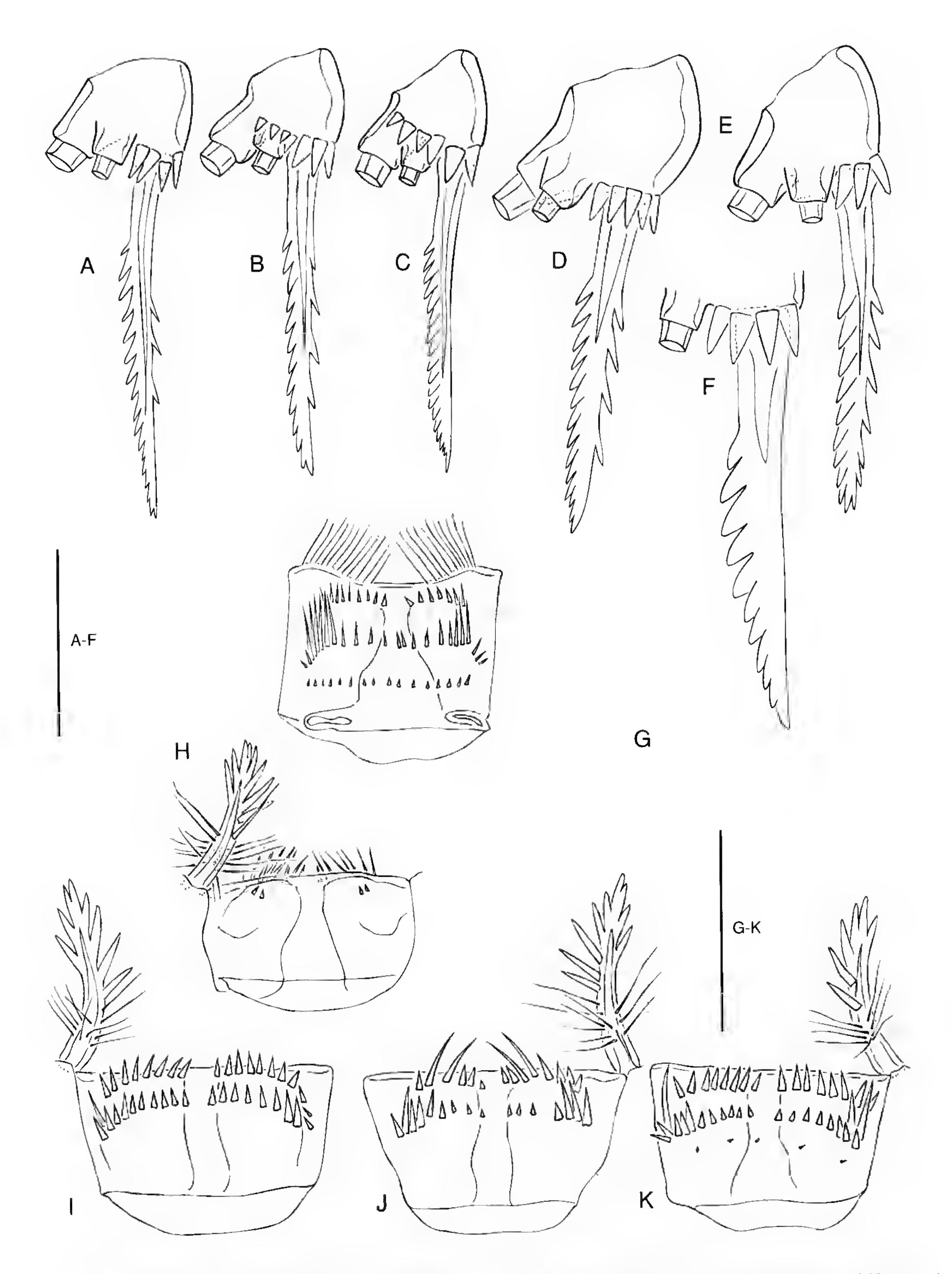


FIG. 6. — *P. fimbriatus*; non-type, adult ♀; **A-C**, leg 5, ventral (India); **D**, **E**, leg 5, ventral (St Petersburg); **F**, leg 5, ventral (Germany); **G**, leg 3, intercoxal sclerite, posterior (Lake Baikal); **H** (anterior), **I** (posterior), leg 4, intercoxal sclerite (Russia); **J**, **K**, leg 4, intercoxal sclerite, posterior (India). Scale bars: A-F, 25 µm; G-K, 50 µm.

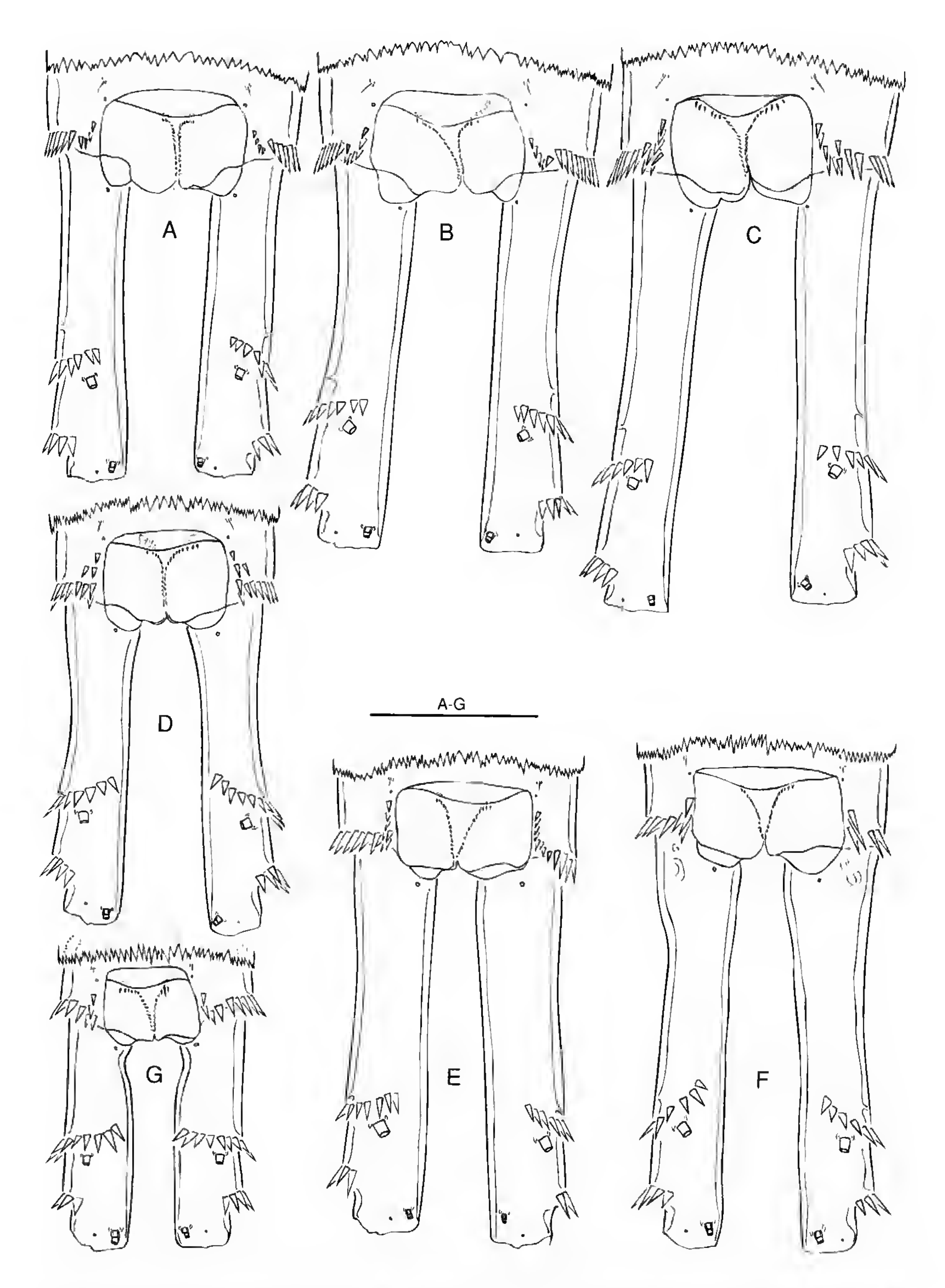


FIG. 7. — *P. fimbriatus*; **A-F,** non-type, adult ♀; **G**, adult ♂; **A-E** (Europe), **F** (India), caudal rami, dorsal; **G**, caudal rami (India). Scale bar: 50 µm.

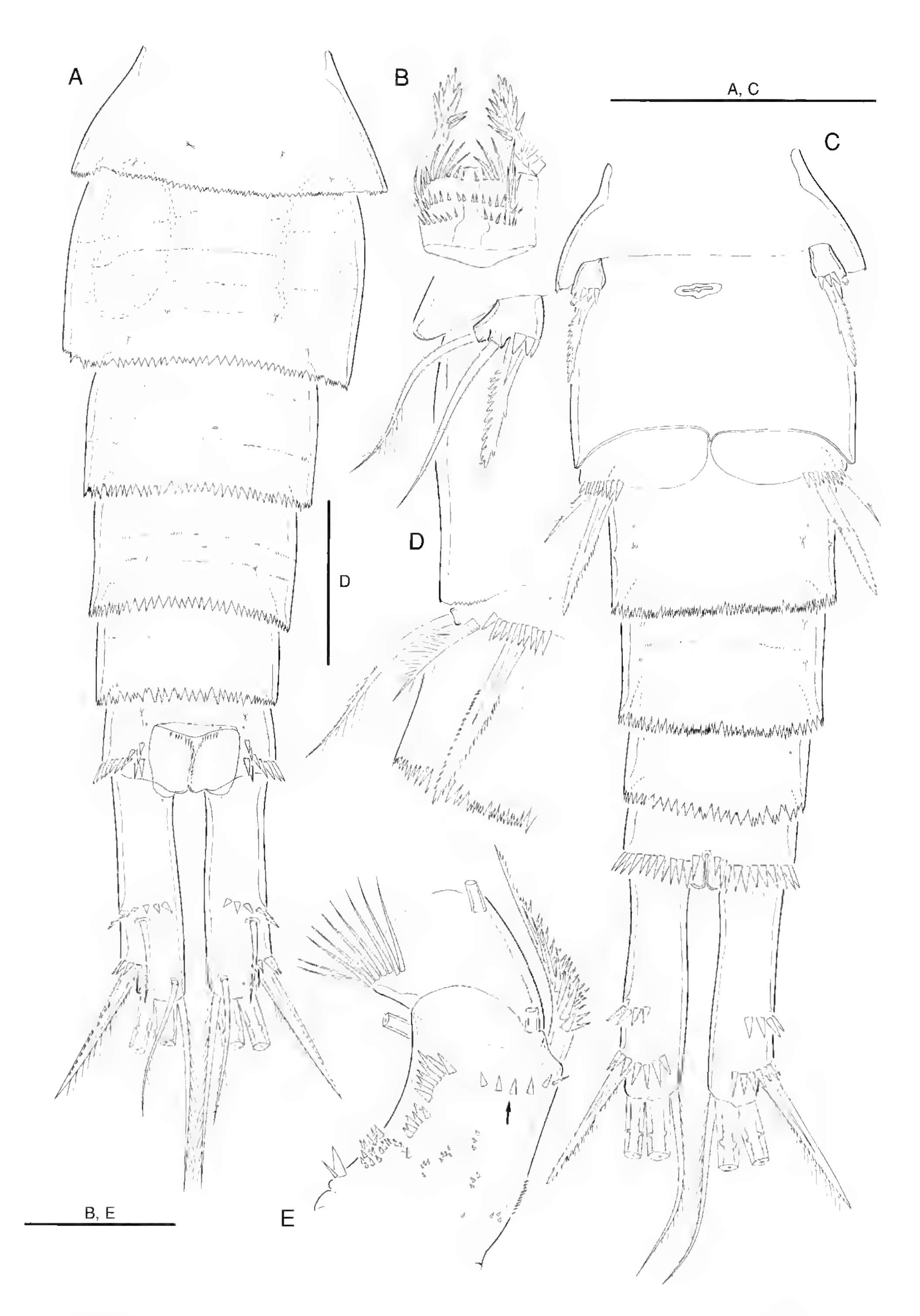


FIG. 8. — *P. fimbriatus*; adult ♂; **A**, urosome, dorsal; **B**, leg 4, intercoxal sclerite, posterior; **C**, urosome, ventral; **D**, detail of leg 5 and leg 6, ventral; **E**, antenna, coxobasis and first endopodal segment, caudal. Scale bars: A, C, 100 µm; B, E, 25 µm; D, 50 µm.

female (Fig. 8D). Sixth leg (Fig. 8D) armed with one inner spine (as long as third urosomal somite and ornamented with about eleven spinules at base) and two outer plumose setae.

Variability

Females

Measurements of body lengths and widths are given in Table 1. One female from St Petersburg possessed an extra spinular row on the anal somite ventrally (Fig. 2D). Specimens from Finland consistently had two spinular rows on exopodal segment 1 of leg 4 on posterior surface (Fig. 5D). These rows appeared inconsistently on specimens from St Petersburg and Turkey. This variability is also illustrated in Damian-Georgescu's (1963) drawings based on material from Romania. The exopodal spines of the swimming legs and the inner spine of leg 5 (Fig. 6F) of some specimens from Oldenburg (Germany) appeared to be stouter than in other populations. Despite the fact that material from Germany had stouter spines on swimming legs, as did the Finish material, the two posterior spinular rows on the first exopodal segment of leg 4 were not consistently present in German material. Additional variability was noted for the spinules on anterior surface of the intercoxal sclerite of leg 3 which may be present or absent in any population examined (Fig. 5F, G) and some specimens from the vicinity of Lake Baikal had three rows of spinules posteriorly on the intercoxal sclerite (Fig. 6G).

Variability in the arrangement and number of posterior spinular rows on the intercoxal sclerite of leg 4, as well as in the shape of the inner coxal spine (degree of curvature) on leg 4 was also noted in some specimens from the vicinity of Lake Baikal (Fig. 6H, I) and from India (Fig. 6J, K). The material from India especially showed interesting variability in leg 5 (*cf.* Fig. 6A-C) as the inner spine was usually longer than in other material examined and there were spinules present at the base of the middle seta in some specimens (Fig. 6B, C). Variability in the structure of the inner spine of leg 5 in specimens from St Petersburg region is shown in Figure 6D, E, but no consistent pattern was observed in this variability.

Males

In material from Japan, a group of spinules (arrowed in Fig. 8E) on the coxobasis of antenna can be very small or absent in some specimens.

Differential diagnosis

P. fimbriatus is distinguished by the following unique combination of characters: the structure of leg 5 (Fig. 2C), the spinular ornamentation of coxobasis of antenna in both sexes (Figs 3B, C, 8E), the structure of the receptaculum seminis (Fig. 2B), the absence of the aesthetasc on the first segment of the male antennule (Fig. 9A).

P. fimbriatus and *P. imminuta* are easily confused as a result of their close morphological similarity. Nevertheless, the absence of the well-developed spinular row on the frontal surface of the coxobasis of the antenna in *P. fimbriatus* (Fig. 3C) can be used unequivocally to separate females of *P. fimbriatus* from *P. imminuta*. The spinular row is sexually dimorphic and, in the adult male of *P. fimbriatus* (Fig. 8E), the spinules are less well-developed than in *P. imminuta* (arrowed in Fig. 15D). In addition, the ornamentation of the mid-distal spinular ornamentation on the posterior surface of leg 1 in *P. imminuta* is significantly different (arrowed in Fig. 13B) from that of *P. fimbriatus* (Fig. 4F). *P. fimbriatus* can easily be separated from *P. chiltoni* by the length of outer seta of leg 5 in the female (Fig. 2C), by the absence of cuticular depressions on the ventral surface of the caudal rami in the female and by the structure of the seminal receptacle (Fig. 2B).

Remarks

Most early descriptions of this species lack detail and several subspecies have been described on the basis of characters that are very variable. Most early records are, therefore, unreliable. Below, comparisons are made only with the important descriptions that conform to *P. fimbriatus* as described above. However, one record of "*P. fimbriatus*" from Iran (Lindberg 1941) should be mentioned here because the material described by Lindberg appears to be significantly different from the typical form described in detail above, on the basis of very short inner spine of leg 5 (Lindberg 1941: 477, figs a, e). This record does



FIG. 9. — *P. fimbriatus*; adult ♂, antennule; **A**, anteroventral showing setation; **B**, terminal segment, posterior; **C**, ventral showing segmentation; **D**, dorsal showing segmentation; **E**, first segment showing setation, anteroventral. Scale bars: A, B, 25 µm; C-E, 50 µm.

not conform to *P. fimbriatus* as defined here and may represent a new species.

After Fischer (1853), a more detailed description of *P. fimbriatus* was given by Brady (1878). In Brady's drawings the caudal rami are inserted very wide apart. This character is typical of *P. fimbriatus* and is never found in *P. imminuta*. Later, further improved illustrations were provided by Schmeil (1892) showing long caudal rami, the structure of leg 5 and the seminal receptacle. These characters, though variable, help to confirm the identity of his material as *P. fimbriatus*. After Schmeil, similar descriptions were given by Sars (1913-1918) as *Platycyclops fimbriatus* and by Pesta (1928) under the name *Cyclops* (*Paracyclops*) *fimbriatus*.

Although Kokubo (1912) presumably overlooked the third seta of leg 5 or possibly examined an aberrant specimen, his description of *Cyclops soli* indicates that it is a synonym of *P. fimbriatus*.

Kiefer (1929) separated *P. abnobensis* from *P. fimbriatus* on the basis of shorter (not quite 4 times as long as broad) but widely separated caudal rami. In addition, in leg 4 the inner apical spine is twice as long as the third endopodal segment and the outer seta of leg 5 is relatively long. These characters do not differ significantly from those of *P. fimbriatus*. It is now widely accepted that the length of caudal rami is a very variable feature within species of Cyclopidae in general. Individual examination of specimens in samples of *P. fimbriatus* from several localities in Europe, especially those specimens with short caudal rami (see Fig. 7A), revealed no consistent variation in characters other than length of caudal rami to support the validity of *P. abnobensis*. Consequently, *P. abnobenis* is treated here as a synonym of *P. fimbriatus*, following Dussart & Defaye (1985). Variation in the length of caudal rami was also indicated by Monchenko's (1974) description of *P. fimbriatus* in which the caudal rami are shown as very short and widely separated.

Lindberg (1939) described *P. vagus* as a new species from India but later synonymized it with *P. fimbriatus* (Lindberg 1958). Study of material from India that was identified as *P. vagus* by Ranga Reddy & Radhakrishna (1984) revealed variation in leg 5 (*cf.* Fig. 6A-C), as the inner spine was usually longer than in other material examined and there were spinules present at the base of the middle seta in some specimens (Fig. 6B, C). Consistent variation, however, was not observed and no additional characters supporting the status of *P. vagus* as a distinct species or subspecies were found. In accordance with Lindberg (1958) *P. vagus* is treated here as a synonym of *P. fimbriatus*.

Paracyclops imminuta Kiefer, 1929
(Figs 10-16)

Original description:
Paracyclops fimbriatus f. *imminuta* Kiefer, 1929 [Zur Kenntnis einiger Artgruppen der Süsswasser-Cyclopiden. *Z. wiss. Zool.* 133: 1-56, figs 1-61].

Synonymy:
Cyclops fimbriatus Fischer var: Kiefer, 1926: 278.

Paracyclops fimbriatus f. *imminuta* Kiefer, 1929: 49, 50, Abb. 54-56.

Paracyclops fimbriatus Fischer, 1853 *sensu* Gurney 1933: 121-126, figs 1438-1458.

Paracyclops fimbriatus orientalis Alekseev, 1995: 133-138, figs 1, 2.

TYPE LOCALITY. — Germany: Mains water system of Oefingen (Kiefer 1929).

MATERIAL EXAMINED. — It has not been possible to examine the type material of *Paracyclops fimbriatus* f. *imminuta* Kiefer, 1929. It is not listed in the catalogue of the Kiefer collection (Franke 1989) and may not be extant.

England. Co. Durham: 26 ♀♀, 10 ♂♂ (Norman Collection, NHM 1911.11.8.40884-903). — Richmond Park, Surrey, 5.VI.1967, coll. A. J. Bruce: 9 ♀♀, 3 ♂♂ (NHM 1967.9.1.242). — Rainton Meadows, Durham: 34 ♀♀, 11 ♂♂ (Norman Collection, NHM 1900.3.29.261). — Somerset: 2 ♀ (NHM 1953.6.29.1). — Beechwood Park: 1 ♀ (NHM 1965.4.1.1.5). — Langness Cave, Deep Threshold, partly dried up pool, pH 6.7, t 21.5 °C, conductivity 725 ms/cm, coll. M. Moseley: 3 ♀♀. — Highgate: 3 ♀♀ (NHM 1951.11.9.3). — Derby Power Station: 1 ♀ (NHM 1963.7.16.3). — Manchester: 2 ♀♀, 1 ♂ (NHM 1961.3.10.1). — Langness Peninsula (NGR SC 281653) from damp pebble/gravel on floor, 2"-3" below ground, (material was collected from a sea cave which is only inundated by the sea during storms, freshwater enters as seepage at other times), 30.VII.1994: 3 ♀♀, 4 ♂♂.

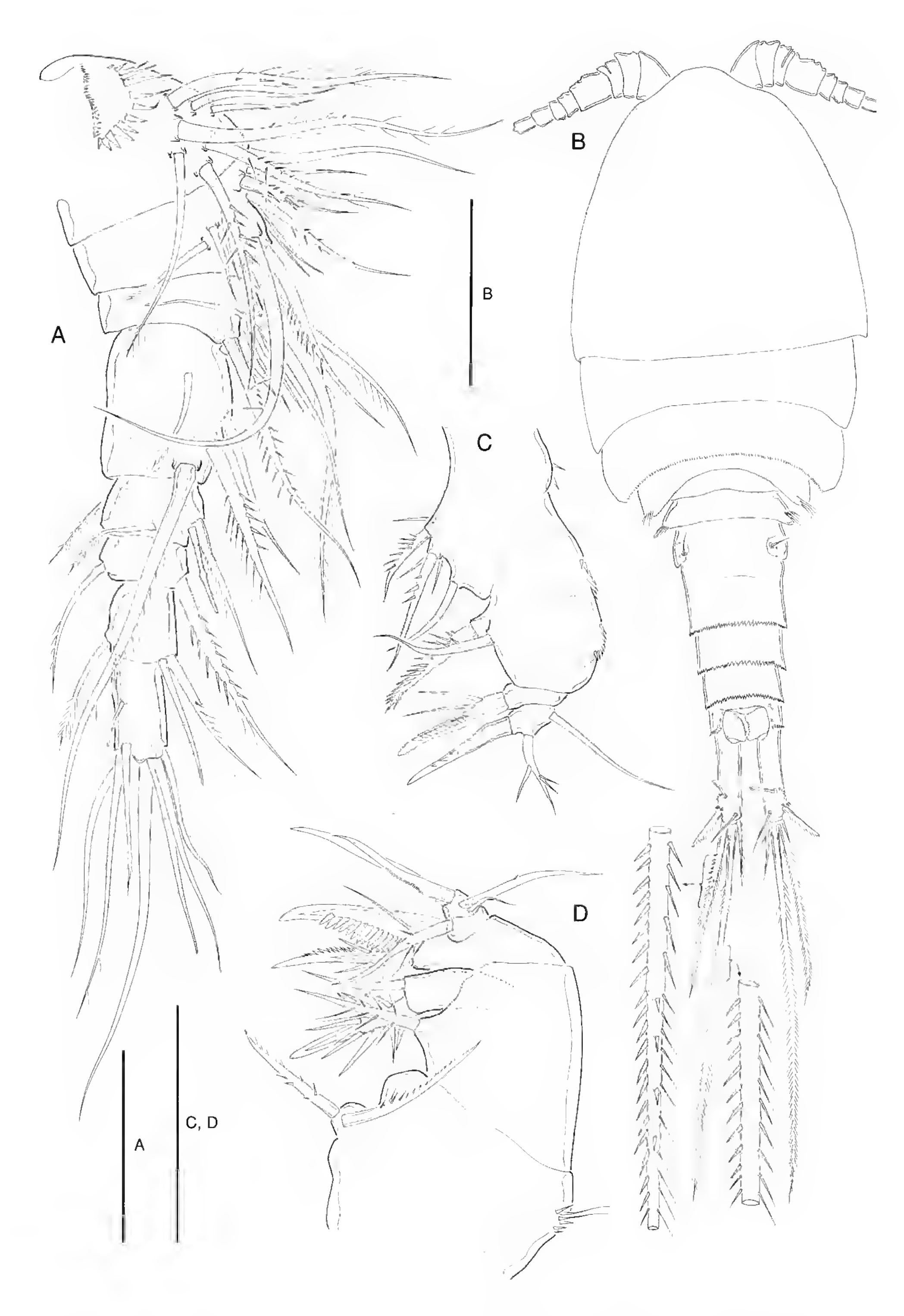


FIG. 10. — *P. imminuta*; adult ♀; **A**, antennule; **B**, body, dorsal; **C**, maxilliped; **D**, maxilla. Scale bars: A, C, D, 50 µm; B, 200 µm.

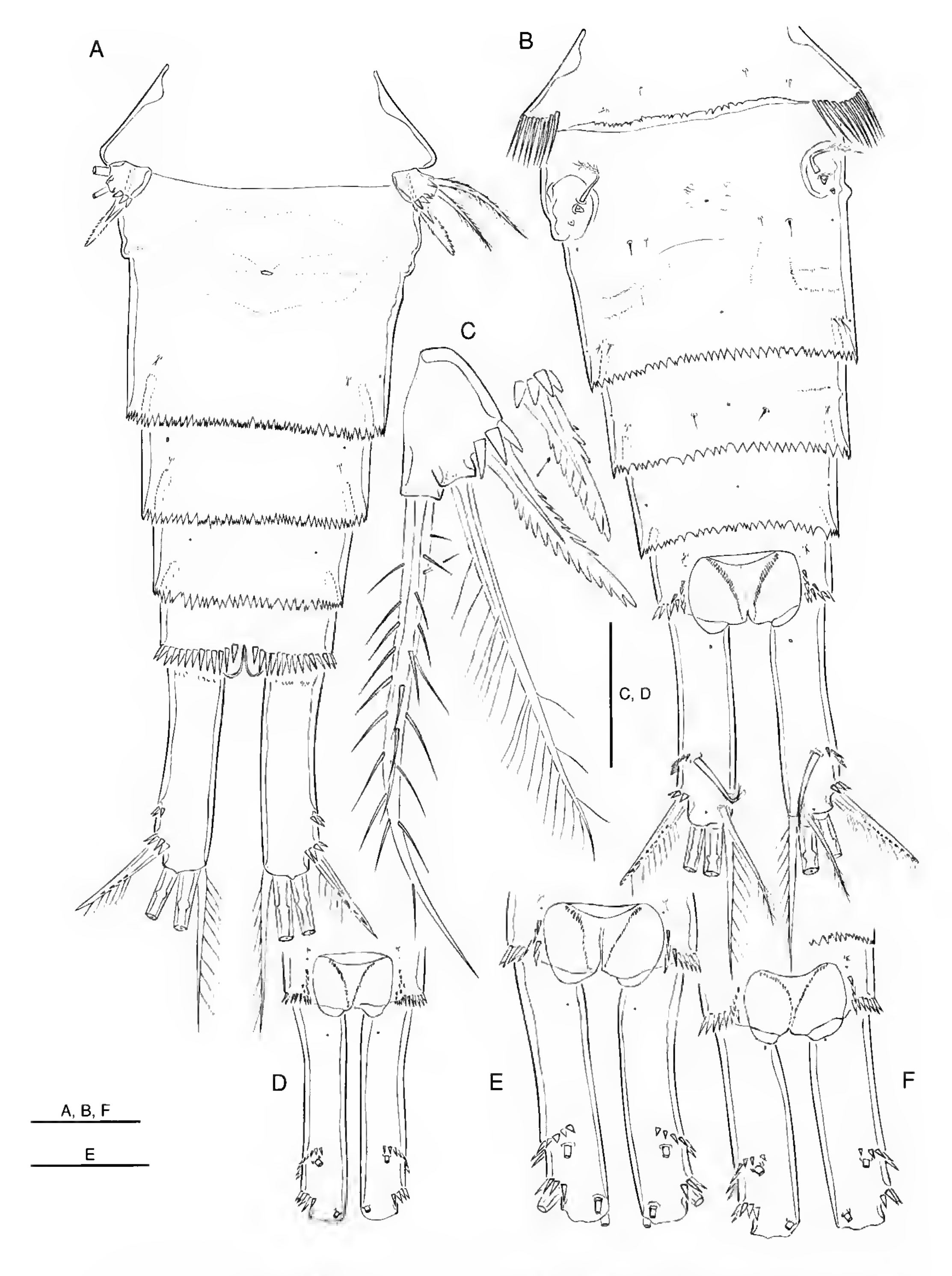


FIG. 11. — *P. imminuta*; adult ♀; **A**, urosome, ventral; **B**, urosome, dorsal; **C**, leg 5, ventral; **D-F**, caudal rami, dorsal. Scale bars: A, B, F, 50 µm; C, D, 25 µm; E, 100 µm.

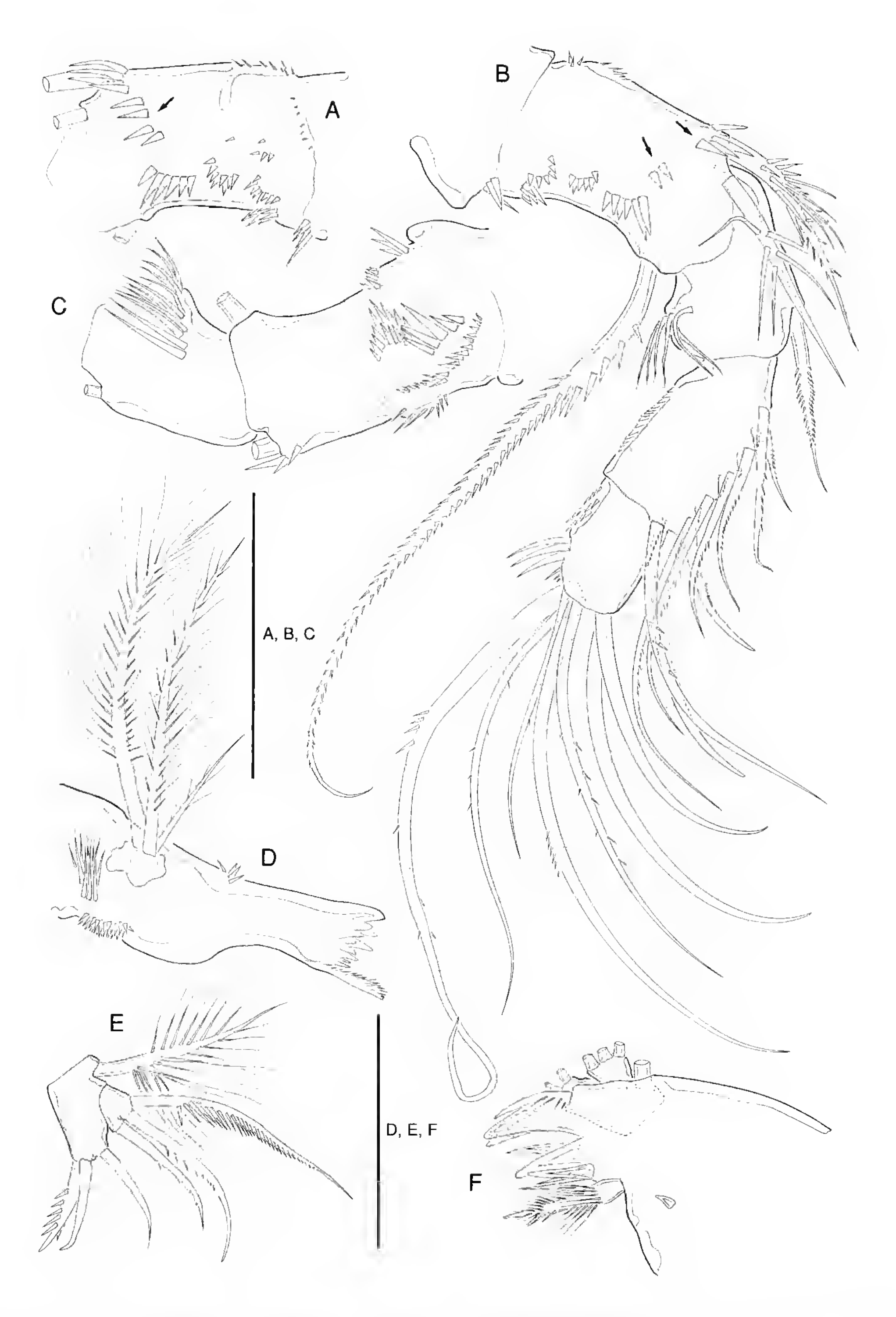


FIG. 12. — *P. imminuta*; adult ♀; **A**, antenna, coxobasis showing variant pattern of spinulation, caudal; **B**, antenna, caudal; **C**, antenna, coxobasis and first endopodal segment, frontal; **D**, mandible; **E**, maxillulary palp; **F**, maxillule. Scale bars: 50 µm.

Russia. River Igora (Neva system), about 10-15 km east of St Petersburg, 22.VII.1996, depth 0.5 m, t 18 °C, coll. V. Alekseev: 1 ♀. — P. Dudergofka, St Petersburg, 27.VII.1996, depth 0.5 m, t 18 °C, coll. V. Alekseev: 1 ♀. — St Petersburg water supply system pond, August 1984, coll. V. Alekseev: 2 ♀♀.
Ireland. Several females and males selected from more than 200 specimens (Norman Collection, NHM 1911.11.8.40915-934).
Norway. 69 ♀♀, 16 ♂♂ (G. O. Sars Collection, ZM F20478; no locality is given by G. O. Sars on the original label but on a second label is written: "Norv", which indicates that the material is probably from Norway; this material contains a mixture of *P. fimbriatus* and *P. imminuta*.).
Sweden. Lake Malar, Upland: 4 ♀♀, 2 ♂♂ (Norman Collection, NHM 1911.11.8.40935-939).
Greece. Delphi: 1 ♀, 1 ♂ (Gurney Collection, NHM 1937.11.16.620-1).
Israel. 3 ♀♀ on two slides (Glassman Collection; En Qumran, IES cop 226301); 1 ♀ on 1 slide (Glassman Collection; En Ziv, IES cop 200701).
Azores. Pico, 12.X.1971: 2 ♀♀ dissected on three slides (Th. Monod Collection n° 15190, MNHN); 2 ♂♂ mounted on one slide (Th. Monod Collection n° 15188, MNHN). — Terceira, 15.X.1971: 1 ♀

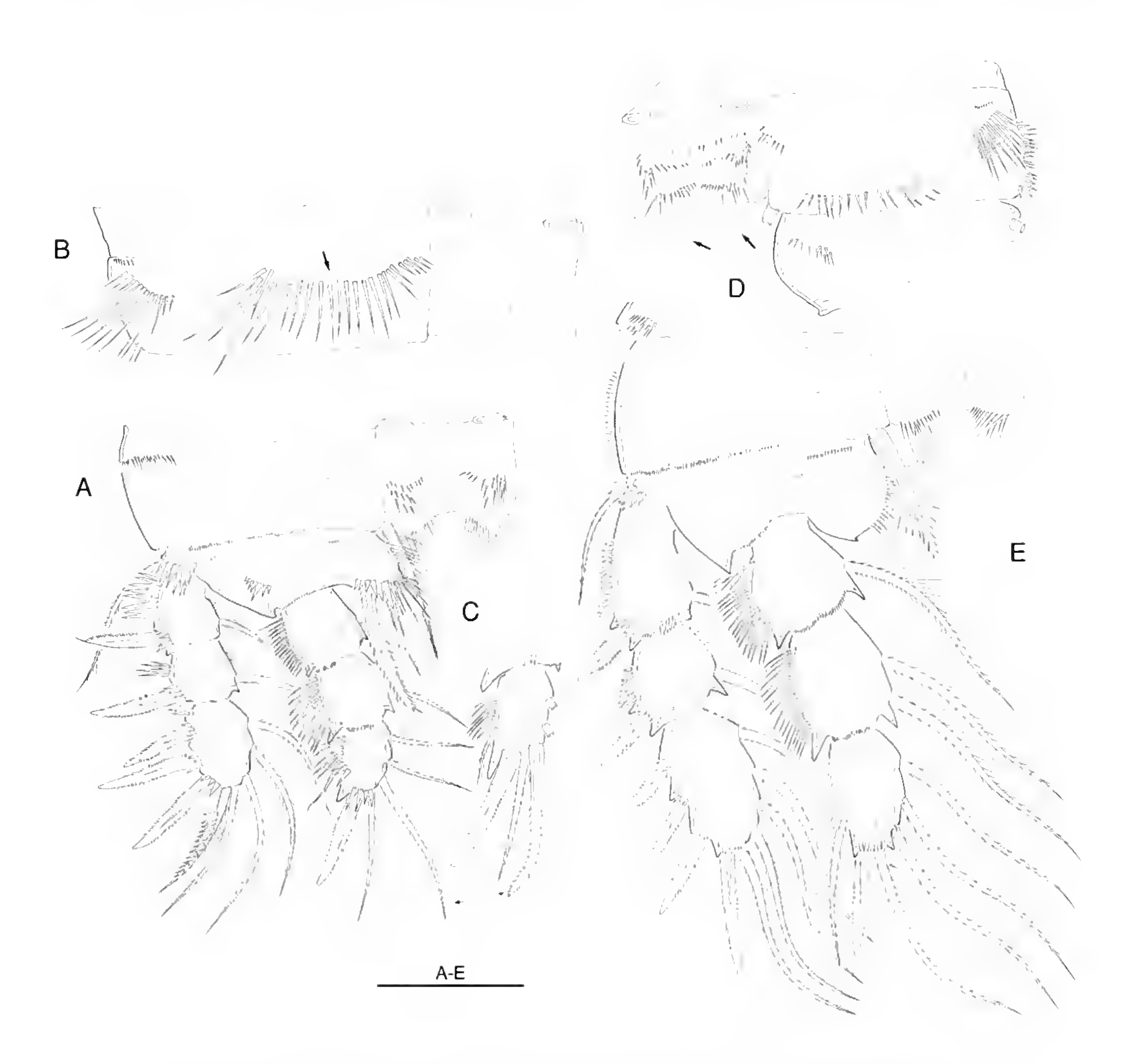


Fig. 13. — *P. imminuta*; **A**, **B**, **D**, **E**, adult ♀; **C**, adult ♂; **A**, leg 1, anterior; **B**, intercoxal sclerite and coxa of leg 1, posterior; **C**, terminal endopodal segment of leg 1; **D**, intercoxal sclerite and coxa of leg 3, posterior; **E**, leg 3, anterior. Scale bar: 50 µm.

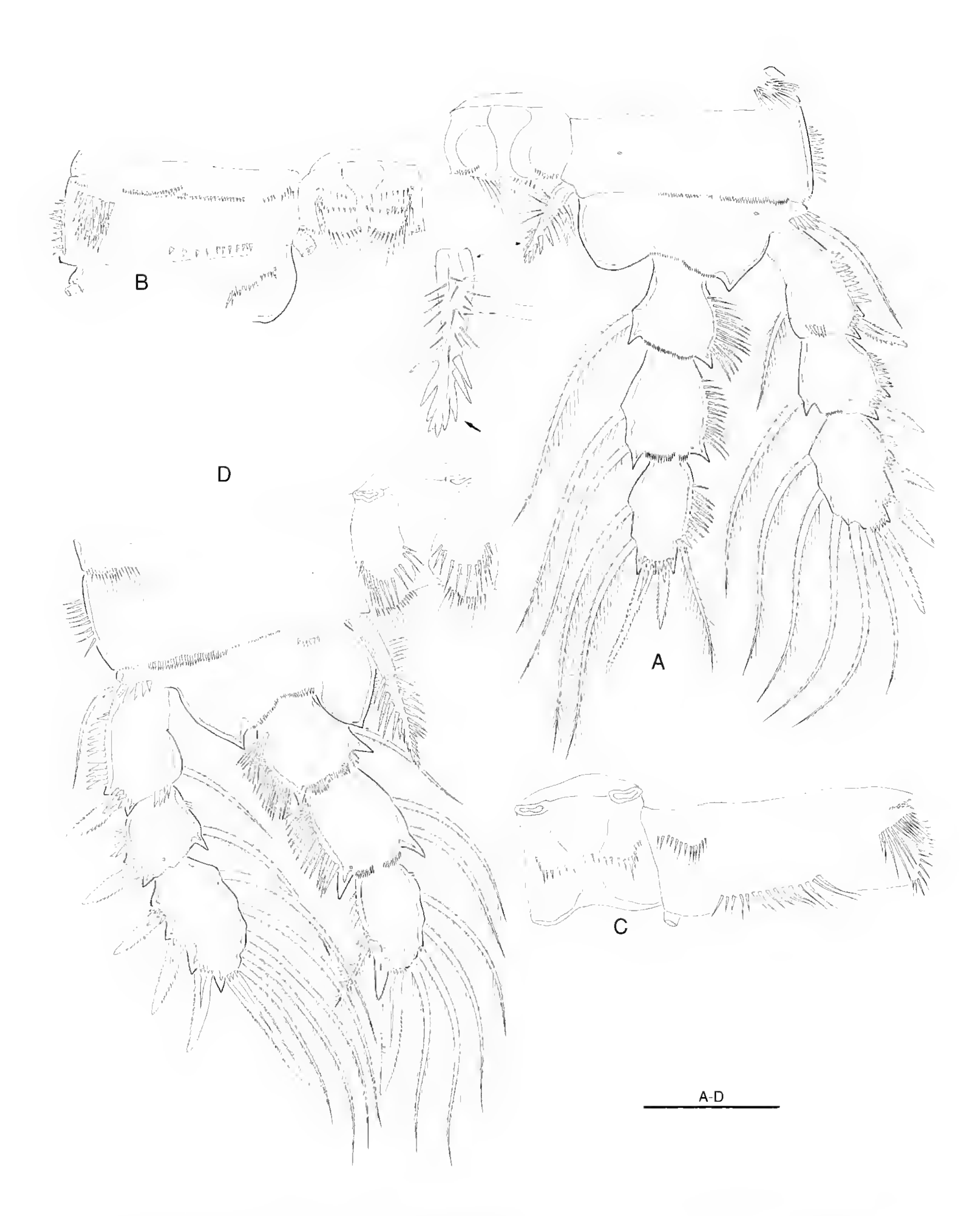


FIG. 14. — *P. imminuta*; adult ♀; **A**, leg 4, anterior; **B**, intercoxal sclerite and coxa of leg 4, posterior; **C**, intercoxal sclerite and coxa of leg 2, posterior; **D**, leg 2, anterior. Scale bar: 50 µm.

dissected on one slide (Th Monod n° 15208, MNHN Collection).
Gibraltar. Leonora Cave, from pool with rotten rope in it: 1 ♀, 5 ♂♂ (NHM 1958.8.5.1).
France. Lac Léman, August 1962, coll. B. Dussart: 3 ♀♀ (MNHN-Cp897).

DISTRIBUTION. — On the basis of examined material only, the distribution of *P. imminuta* extends across Europe to central Russia, and southwards to include Israel.

REDESCRIPTION

Adult female

Body lengths and widths are given in Table 2. Urosome ornamented with finer surface pits dorsally than *P. fimbriatus* as figured (compare Figs 11A, B and 2A). Genital double-somite hardly increasing in width anteriorly, whereas in *P. fimbriatus* genital-double somite increasing in width anteriorly. Seminal receptacles divided into broad anterior and narrower posterior lobes (Fig. 11A), lobes narrower and more distinctly separated than those of *P. fimbriatus*. Caudal rami positioned in parallel configuration, and frequently very close to each other; in some specimens slightly converging proximally, parallel distally (Fig. 11A, B, D-F).
Coxobasis of antenna with complex ornamentation on caudal and frontal surfaces as figured (Fig. 12A-C); well-developed spinular row present on caudal surface (arrowed in Fig. 12A, B).
Coxa of leg 1 ornamented with long continuous spinular row across posterior surface (arrowed in Fig. 13B). Intercoxal sclerite ornamented with group of spinules on anterior surface (Fig. 13A). Leg 3 (Fig. 13E) with intercoxal sclerite ornamented with three spinular rows on posterior surface (Fig. 13D); distal row of spinules (arrowed in Fig. 13D) longer than that of *P. fimbriatus*. Leg 4 with inner coxal spine slightly stouter than that of *P. fimbriatus* (Fig. 14A); distal spinular row on posterior surface of intercoxal sclerite hair-like and much longer than that of *P. fimbriatus* (Fig. 14B); inner apical spine of endopodal segment 3 as long as segment, ratio of length of inner apical spine relative to outer apical spine usually smaller than in *P. fimbriatus*.

Spine and seta formula as follows:

	Coxa	Basis	Exopod	Endopod
Leg 1	0-1	1-I	I-1; I-1; III, 5	0-1; 0-1; 1, I, 4
Leg 2	0-l	1-0	I-1; I-1; III, I, 5	0-1; 0-2; 1, I, 4
Leg 3	0-l	1-0	I-1; I-1; III, I, 5	0-1; 0-2; 1, I, 4
Leg 4	0-l	1-0	I-1; I-1; II, I, 5	0-1; 0-2; 1, II, 2

Leg 5 with inner spine serrate-like, usually stouter than in *P. fimbriatus* (Fig. 11C). Leg 6 (Fig. 11B) represented by one plumose seta and two tiny spinules located dorsolaterally.

Adult male

Body lengths and widths excluding caudal setae are given in Table 2. Differing from adult female as follows: urosomal somites (Fig. 15C) ornamented with cuticular pits dorsally as figured. Caudal rami slightly curved inwards proximally, usually parallel for most of length. Coxobasis of antenna with spinular row near base of inner setae (arrowed in Fig. 15D). Innermost seta of coxobasis more strongly spinulated than in female (arrowed in Fig. 15D). Antennule similar to that of male *P. fimbriatus* except aesthetasc on first segment (arrowed in Fig. 16E, F) present and setiform. Aesthetasc on ancestral segment XIV much longer than in *P. fimbriatus* (arrowed in Fig. 16E). Segmental fusion pattern as follows: I-V, VI-VII, VIII, IX, X, XI, XII, XIII, XIV, XV, XVI, XVII, XVIII-XX, XXI-XXIII, XXIV-XXVIII.

VARIABILITY

Females

The relative width, length and shape of caudal rami can vary between specimens from any population as illustrated in figure 11B, D-F. The arrangement of the spinular row on the caudal surface of the antenna (arrowed in Fig. 12A, B) may also vary slightly. The length ratio of the outer apical spine relative to the inner apical spine on the distal endopod segment of leg 4 can be very variable. The form and length of the inner spine of leg 5 can also be variable with some populations or individuals having a stouter spine (Fig. 11C) than others.

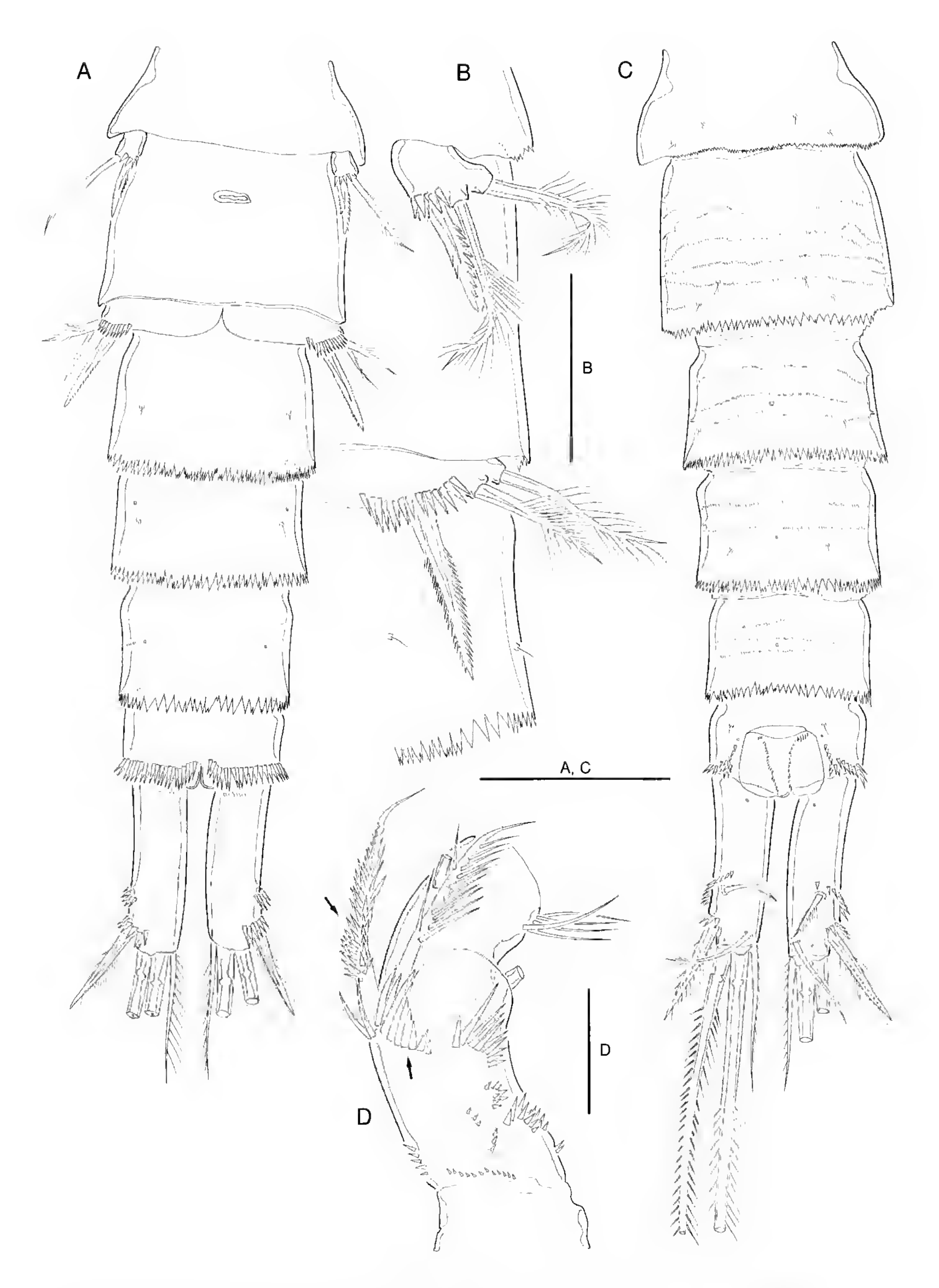


FIG. 15. — *P. imminuta*; adult ♂; **A**, urosome, ventral; **B**, detail of leg 5 and leg 6, ventral; **C**, urosome, dorsal; **D**, antenna, coxobasis and first endopodal segment, caudal. Scale bars: A, C, 100 µm; B, 50 µm; D, 25 µm.

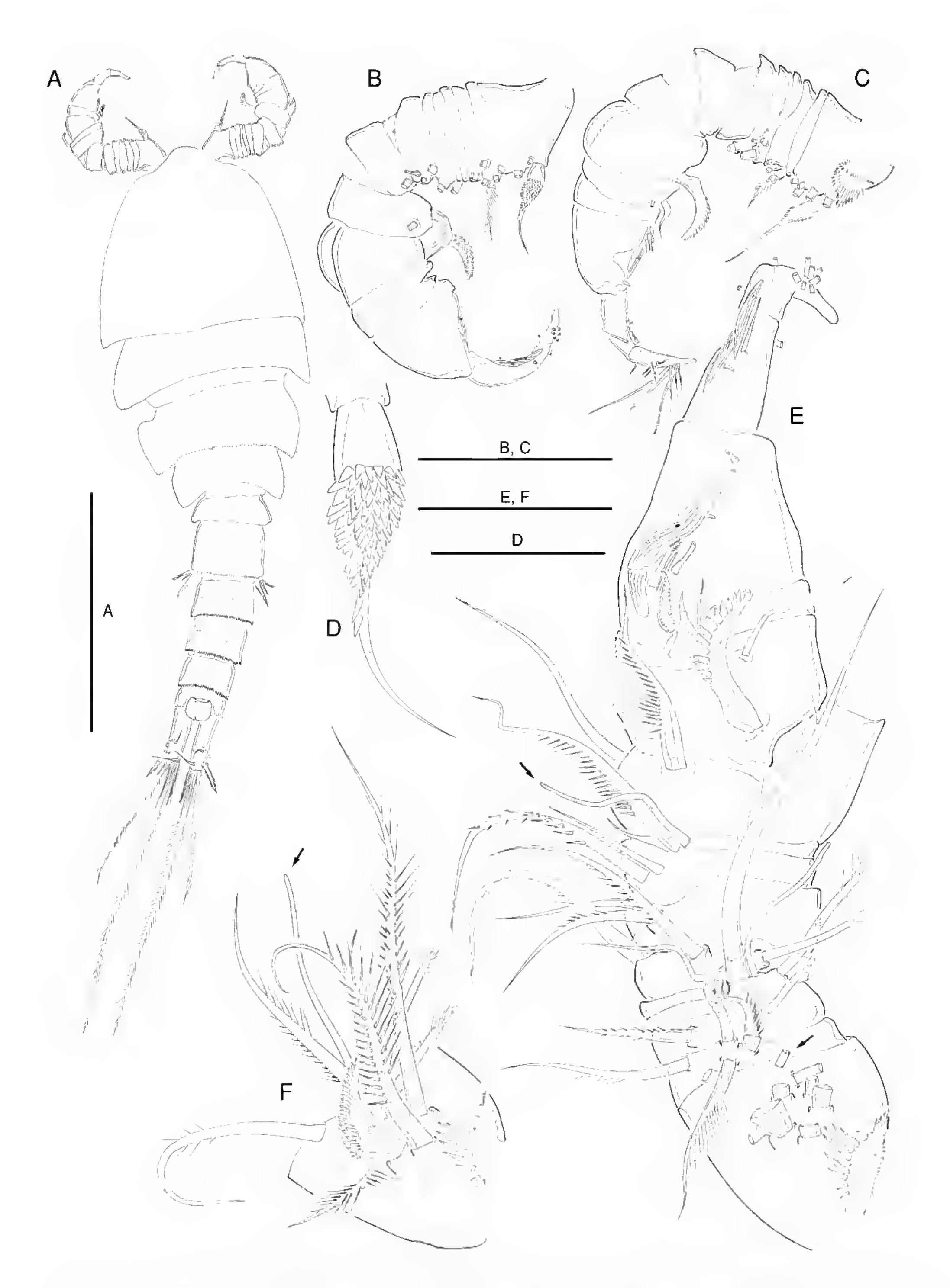


FIG. 16. — *P. imminuta*, adult ♂; **A**, body, dorsal; **B**, antennule showing segmentation, dorsal; **C**, antennule showing segmentation, ventral; **D**, detail of modified seta on first segment of the antennule; **E**, antennule showing setation, anteroventral; **F**, antennule, first segment showing setation, anteroventral. Scale bars: A, 400 µm; B, C, 100 µm, D, 25 µm; E, F, 50 µm.

Table 2. — Body length (BL) and width (BW) measurements (in µm) of adult *Paracyclops imminuta* from different localities (N, number of specimens measured).

LOCALITY	SEX	BL (mean ± SD)	RANGE	BW (mean ± SD)	RANGE	N
St Petersburg	♀	846 ± 26.2	827-864	310 ± 1.4	309-311	2
England	♀	1014 ± 51.7	918-1082	343 ± 15.4	305-359	10
	♂	960 ± 60.3	872-1079	321 ± 23.6	275-354	10
Ireland	♀	835 ± 32	781-880	318 ± 14.2	293-342	10
	♂	805 ± 30.6	757-858	292 ± 9.4	282-311	10
Sweden	♀	1072 ± 128.7	981-1163	351 ± 23.3	334-367	2
	♂	819		299		1
Greece	♀	670		247		1
	♂	670		243		1
Azores (Pico)	♂	791 ± 74.2	738-843	298 ± 7.1	293-303	2
Israel	♀	777 ± 82.7	718-835	286 ± 1.4	285-287	2
Gibraltar	♂	910 ± 37	849-946	292 ± 7.5	280-301	5
France	♀	921 ± 143.8	835-1087	315 ± 25.4	299-344	3

Differential diagnosis

The close morphological similarity between *P. fimbriatus* and *P. imminuta* makes it easy to confuse them, however, there are two characters that have proven to be extremely constant both within and between populations of *P. imminuta*. These characters are the spinular ornamentation on the caudal surface of the antennary coxobasis (arrowed in Fig. 12A, B) and the presence of the mid-distal spinular row on the posterior surface of leg 1 (arrowed in Fig. 13B). The latter character also distinguishes *P. imminuta* from other *Paracyclops* species. In addition, the following combination of five characters also separates *P. imminuta* from *P. fimbriatus*: (1) the spinular row near the base of inner setae on the coxobasis of antenna which is better developed in the male of *P. imminuta* (arrowed in Fig. 15D) than in *P. fimbriatus* (Fig. 8E); (2) the aesthetasc on the first segment of male antennule (arrowed in Fig. 16E, F) which is present only in *P. imminuta*; (3) the inner coxal spine of leg 4 (Fig. 14A), which is stouter than in *P. fimbriatus*; (4) the form of the distal spinular row on the posterior surface of the intercoxal sclerite of legs 3-4 (Fig. 14A, B), the spinules of which are hair-like and much longer than in *P. fimbriatus*; (5) the aesthetasc on ancestral segment XIV (arrowed in Fig. 16E) which is much longer than that of *P. fimbriatus*.

Remarks

Kiefer (1929) first separated this form from *P. fimbriatus* on the basis of the shorter caudal rami which are about 3-4 times longer than broad. *P. fimbriatus* forma *imminuta* sensu Šramek-Hušek (1939), *Paracyclops fimbriatus* var. *imminutus* sensu Rylov (1963) and *Paracyclops fimbriatus* f. *imminutus* sensu Štěrba (1955) may be considered as conspecific with *P. imminuta* on the basis of the caudal rami which are illustrated as being close to each other and slightly converging in the proximal part. The usefulness of this character is however limited since it is known to be extremely variable.

Borutzky's (1930) usage of the caudal rami and the leg 5 of male in his identification of *P. fimbriatus*. f. *imminuta* is very doubtful since Kiefer did not refer to male characters in his original drawings. Perhaps the most complete description of *P. imminuta* was given by Gurney (1933) under the name *P. fimbriatus*. Fortunately, Gurney figured the coxa of leg 1 in posterior view and it can be seen that the pattern of the spinular row is very similar to that of *P. imminuta* (arrowed in Fig. 13B). Also, there is one relatively large spinule at the base of the outer seta of the antennary coxobasis in the position corresponding to the spinular row in *P. imminuta* (arrowed in Fig. 12A, B) and probably representing the end of this spinular row. As remarked

earlier, these two characters unequivocally separate *P. imminuta* from *P. fimbriatus* and strongly indicate that Gurney's material belonged to the former species. In addition, other less significant characters which serve to separate *P. imminuta* from *P. fimbriatus* can be observed in Gurney's drawings, such as the shape of the caudal rami in both sexes, the structure of the seminal receptacle and the relatively short inner spine on the female leg 5 (Fig. 11C), all of which are more characteristic for *P. imminuta* than *P. fimbriatus*.

The validity of *P. fimbriatus orientalis* is problematic. This subspecies was incompletely described (Alekseev 1995). Apart from the spinular ornamentation on the coxobasis of the antenna, the illustrations of this species lack sufficient detail. No type material was designated by Alekseev (1995) but four females and three males collected and identified as *P. fimbriatus orientalis* by V. Alekseev were re-examined. None of these specimens matched Alekseev's original drawings of *P. fimbriatus orientalis*. In fact the material represented *P. fimbriatus* and showed variation in the shape of the caudal rami and in the spinular ornamentation on the posterior surface of the intercoxal sclerite of leg 4, as also found in Indian, Mongolian and Uzbekistani material. From the original drawings alone it is extremely difficult to assign *P. fimbriatus orientalis* to any of the species recognised herein. The pattern of spinulation on the coxobasis of antenna is the only indication that Alekseev might have been dealing with the species redescribed here as *P. imminuta*.

Paracyclops chiltoni (Thomson, 1882)
(Figs 17-23)

Original description:
Cyclops chiltoni Thomson, 1882 [*Trans. Proc. New Zealand. Inst.* 15: 93-116].

Synonymy:
Cyclops chiltoni Thomson, 1882: 97, pl. IX, figs 11-19.

Paracyclops finitimus Kiefer, 1929: 51, Abb. 60, 61.

Paracyclops fimbriatus Fischer, 1853 *sensu* Karaytug & Boxshall 1996: 42-66, figs 1-22.

TYPE LOCALITY. — New Zealand, Eyreton.

MATERIAL EXAMINED. — It has not been possible to locate Thomson's type material. It is not stored in the collection of the National Museum of New Zealand. One vial with forty-seven specimens from New Zealand is stored in the Smithsonian Institution, Washington, D. C. The redescription is based on this material.
New Zealand. South Island, Southland, Te Anau, Upakerora River, New Zealand, 45°21'18S - 167°43'18E, 15.IV.1990, coll. T. Ishida: 33 ♀♀, 8 ♂♂, 6 copepodids (USNM. cat. 250692).
Easter Island. Rano Aroi crater (almost completely overgrown by *Polygonum*), small puddle of open water in littoral zone, 19.IX.1990, coll. H. J. Dumont: 2 ♀♀, 21 ♂♂.
South Africa. 52 ♀♀, 44 ♂♂, coll. A. D. Harrison (NHM 1966.3.22.9).
England. Hertfordshire, percolating filters of sewage works: 50 ♀♀, 65 ♂♂ (NHM 1968.7.1.1). — London, Regent's Park pond. Numerous specimens examined from cultured material.
Russia. P. Dudergofka, St Petersburg, 27.VII 1996, depth 0.5 m, t 18 °C, coll. V. Alekseev: 4 ♀♀.
Crozet Island. 28.II.1969: 2 ♂♂ dissected on two slides (NHM 1970.4.30.3).
Tahiti. 20.I.1981: 2 ♀♀, 6 ♂♂ (MNHN, unregistered material).
Brazil. Leaf litter and small quantity of moist superficial soil collected from bank of a rill near to the entrance of Gruta da Tapagem (Tapagem Cave), 24°38'12"S - 48°23'50"W, Eldorado Paulista, State of São Paulo, 31.VIII.1988, coll. Carlos E. F. Rocha: 18 ♀♀, 17 ♂♂ obtained from a culture.
Azores. Terceira, mounted on three slides (undissected), 2 ♀, 1 ♂ (Th. Monod Collection n° 15210, MNHN). — Flores, mounted on one slide (undissected), all Th. Monod Collection: 1 ♀ (n° 15324, MNHN); 2 ♀♀, 1 ♂, mounted on two slides (1 ♀ dissected) (n° 15292, MNHN); 1 ♀, partially dissected on one slide (n° 15079, MNHN); 1 ♀, dissected and mounted on one slide (n° 15087, MNHN); 1 ♀, mounted on one slide (n° 15138, MNHN); 1 ♀, dissected and mounted on one slide (n° 15317, MNHN); 1 ♀, dissected and mounted on one slide (n° 15335, MNHN); 1 ♂, mounted on one slide (n° 15274, MNHN). — Pico, 12.X.1971, coll. Th. Monod: 1 ♀, mounted on one slide (Th. Monod Collection n° 15189, MNHN).

DISTRIBUTION. — *P. chiltoni* shows the widest distribution within the genus *Paracyclops* and is the only true cosmopolitan species at present (Karaytug 1998). It occurs at extremely isolated sites such as Easter Island and Hawaii in the Pacific Ocean, Crozet Island in southern Indian Ocean, and in New Zealand. However records of *P. chiltoni* from some other regions could not be confirmed because material was unavailable.

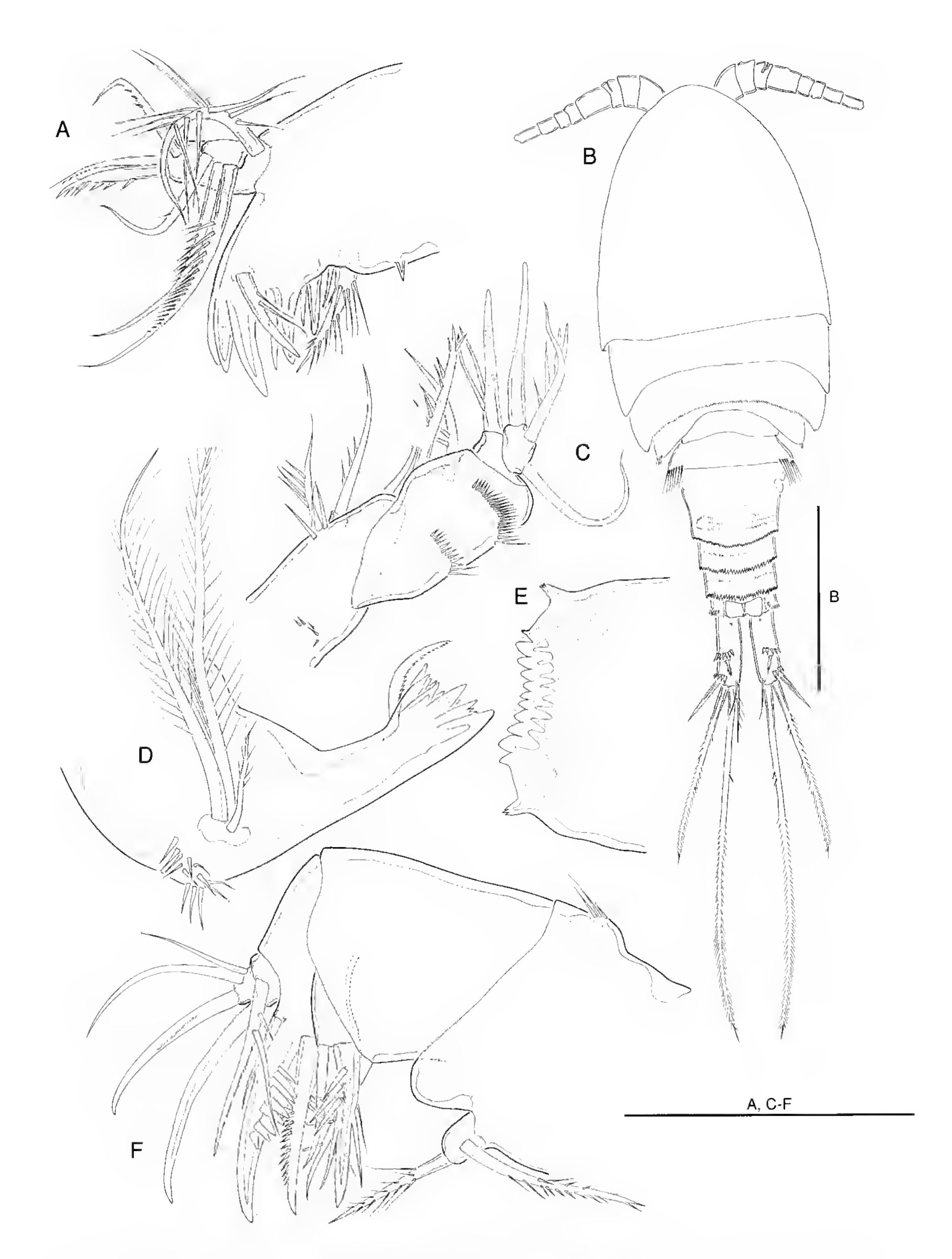


FIG. 17. — *P. chiltoni*; adult ♀; **A**, maxillule; **B**, body, dorsal; **C**, maxilliped; **D**, mandible; **E**, labrum; **F**, maxilla. Scale bars: A, C-F, 50 µm; B, 200 µm.

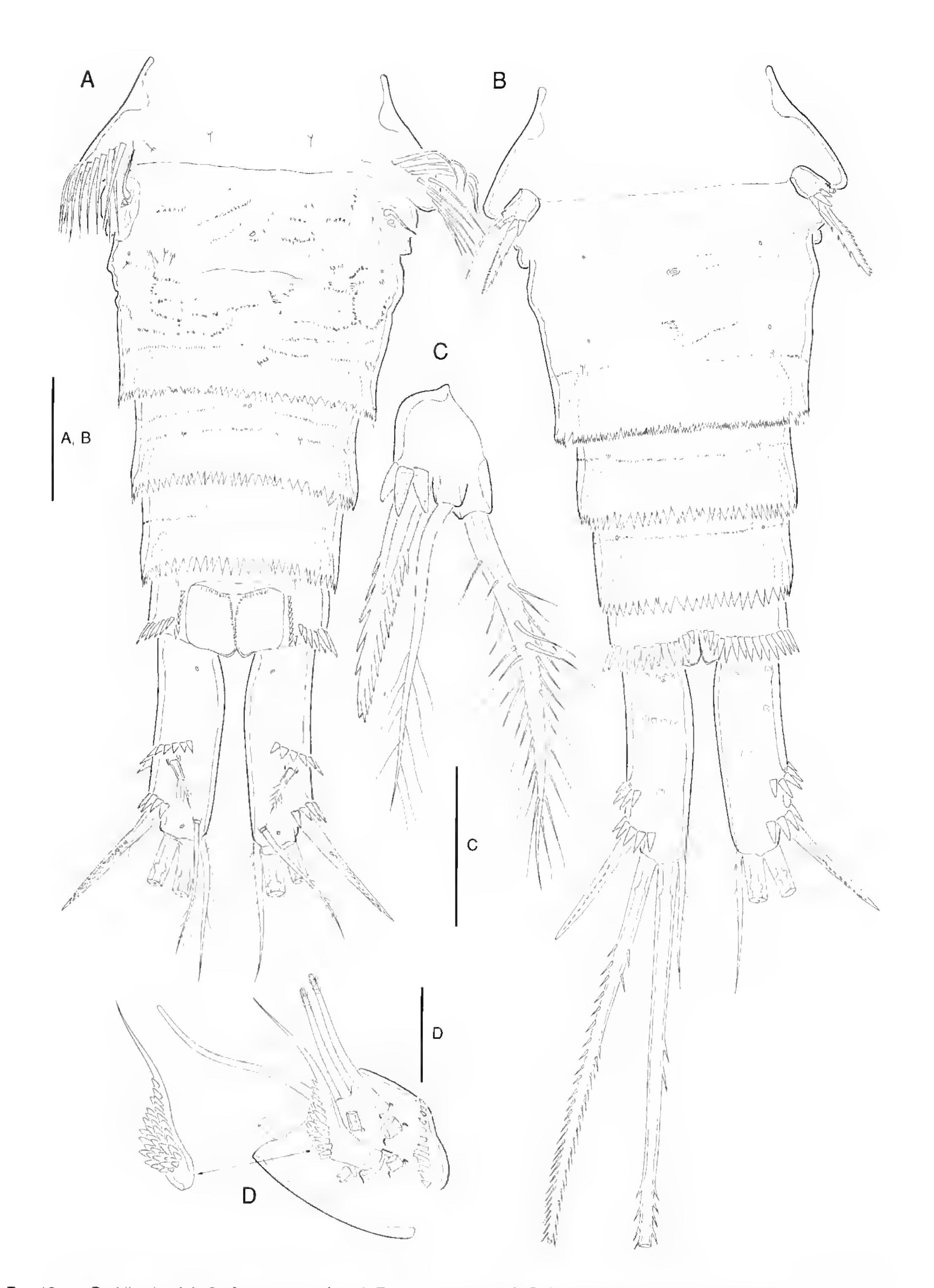


FIG. 18. — *P. chiltoni*; adult ♀; **A**, urosome, dorsal; **B**, urosome, ventral; **C**, leg 5, ventral; **D**, adult ♂, first segment of antennule showing setation, anteroventral, with inset showing detail of modified seta, dorsal. Scale bars: A, B, 50 µm; C, D, 25 µm.



FIG. 19. — *P. chiltoni*; adult ♀; **A**, antenna, coxobasis, frontal; **B**, antenna, caudal; **C**, antennule. Scale bars: A, B, 25 µm; C, 50 µm.

TABLE 3. — Body length (BL) and width (BW) measurements (in μm) of *Paracyclops chiltoni* from different localities. (N, number of specimens measured).

LOCALITY	SEX	BL (mean ± SD)	RANGE	BW (mean ± SD)	RANGE	N
New Zealand	♀	627 ± 36.1	556-738	251 ± 14.9	230-291	30
	♂	581 ± 29.2	531-630	214 ± 5.1	207-222	8
England	♀	713 ± 61.2	588-802	289 ± 24.6	237-353	30
(Hertfordshire)	♂	649 ± 52.5	598-751	240 ± 7.8	227-254	10
Easter Island	♀	555		210		1
	♂	618 ± 22 9	575-664	225 ± 10.9	200-239	12
South Africa	♀	722 ± 49.5	606-798	262 ± 17.9	223-291	14
	♂	655 ± 25.2	606-699	237 ± 8.7	225-252	7
Russia (St Petersburg)	♀	797 ± 68.7	738-857	308 ± 9.8	299-316	4
Tahiti	♀	636 ± 15.6	625-647	232 ± 7.1	227-237	2
	♂	642 ± 25.6	614-676	205 ± 5.4	196-214	6
Brazil	♀	611 ± 42.7	567-703	237 ± 17.8	217-282	10
	♂	548 ± 25.8	505-588	201 ± 12.1	183-217	10

REDESCRIPTION

Adult female

Body width and length are given in Table 3. Genital double-somite, second and third abdominal somites densely ornamented with distinct pits dorsally (Fig. 18A) and ventrally (Fig. 18B) as figured. Genital double-somite about as long as broad; seminal receptacle divided into narrow anterior and broad posterior lobes (Fig. 18B). Row of spinules present in anal cleft either side of midline (Fig 18A). Caudal rami short, parallel, with ornamentation comprising rows of pits or cuticular depressions on ventral surface (Fig. 18B). Length and width of caudal rami from different populations given in Table 4. Antennule 8-segmented (Fig. 19C): setal formula 8, 12, 6, 5, 2 + aesthetasc, 2, 2 + aesthetasc, 7 + aesthetasc. Third segment with two partial suture lines ventrally. Coxobasis of antenna with complex ornamentation on caudal and frontal surfaces as figured (Fig. 19A, B) and lacking spinular row near inner setae caudally (arrowed in Fig. 19B).

Leg 1 intercoxal sclerite ornamented with dense spinules on anterior surface (Fig. 20B). Leg 2 with outer apical spine of distal endopodal segment stout (Fig. 20C); intercoxal sclerite ornamented with dense spinules on anterior surface, single row small spinules on posterior (Fig. 21A). Leg 3 (Fig. 21D, E) intercoxal sclerite ornamented with two spinular rows on posterior surface; inner coxal spine stouter than that of *P. fimbriatus*. Leg 4 (Fig. 21B, C) inner coxal spine stouter than in *P. fimbriatus*; intercoxal sclerite with two spinular

TABLE 4. — Caudal rami length (CL), caudal rami width (CW) and ratio of length relative to width (L:W) of *Paracyclops chiltoni* from different localities (measurements in μm). (N = number of specimens measured).

LOCALITY	SEX	CL (mean ± SD)	RANGE	CW (mean ± SD)	RANGE	N	L:W
New Zealand	♀	79 ± 8.4	68-96	26 ± 1.4	25-30	28	3
England	♀	95 ± 12.8	77-116	28 ± 1.6	26-30	10	3.4
South Africa	♀	94 ± 10.8	78-115	27 ± 1.4	25-29	10	3.5
Russia (St Petersburg)	♀	97 ± 5.9	88-101	25 ± 3.5	20-28	4	3.9
Tahiti	♀	68 ± 14.1	58-78	23 ± 1.4	22-24	2	2.9
Brazil	♀	80 ± 13.5	60-109	25 ± 1.6	23-29	20	3.2
Azores	♀	94 ± 10	84-109	28 ± 1.5	26-30	6	3.4
Easter Island	♀	63		25		1	2.5

rows on posterior surface (Fig. 21C). The outer spinulose seta of leg 5 was equal in length to the inner spine in most specimens from New Zealand and in all specimens examined from other localities (Fig. 22A) but distinctly longer than the inner spine in a few specimens from New Zealand (Fig. 18C).

Adult male
Urosomal somites ornamented with cuticular pits dorsally and ventrally as figured (Fig. 23B, C). Caudal rami about 2.3 times longer than broad. Coxobasis of antenna with well-developed spinular row near base of inner setae (arrowed in Fig. 23E); innermost seta of coxobasis more strongly spinulate than female. First segment of the antennule (Fig. 18D) with large seta and modified by ornamentation of strong spinules in proximal and midsections, tapering to fine point distally (Fig. 18D). First segment with long setiform aesthetasc (Fig. 18D). The setal elements similar to those of *P. imminuta*. Segmental fusion pattern as follows I-V, VI-VII, VIII, IX, X, XI, XII, XIII, XIV, XV, XVI, XVII, XVIII-XX, XXI-XXIII, XXIV-XXVIII.

Variability
Unless stated the following variability applies to the females. The cuticular pits on the ventral surface of the caudal rami may not be as well defined in some specimens from outside the Palaearctic zoogeographical region. The outer spinulose seta of leg 5 was equal in length to the inner spine in most specimens from New Zealand and in all specimens examined from other localities (Fig. 22A) but distinctly longer than the inner spine in a few specimens from New Zealand (Fig. 18C). The structure of the

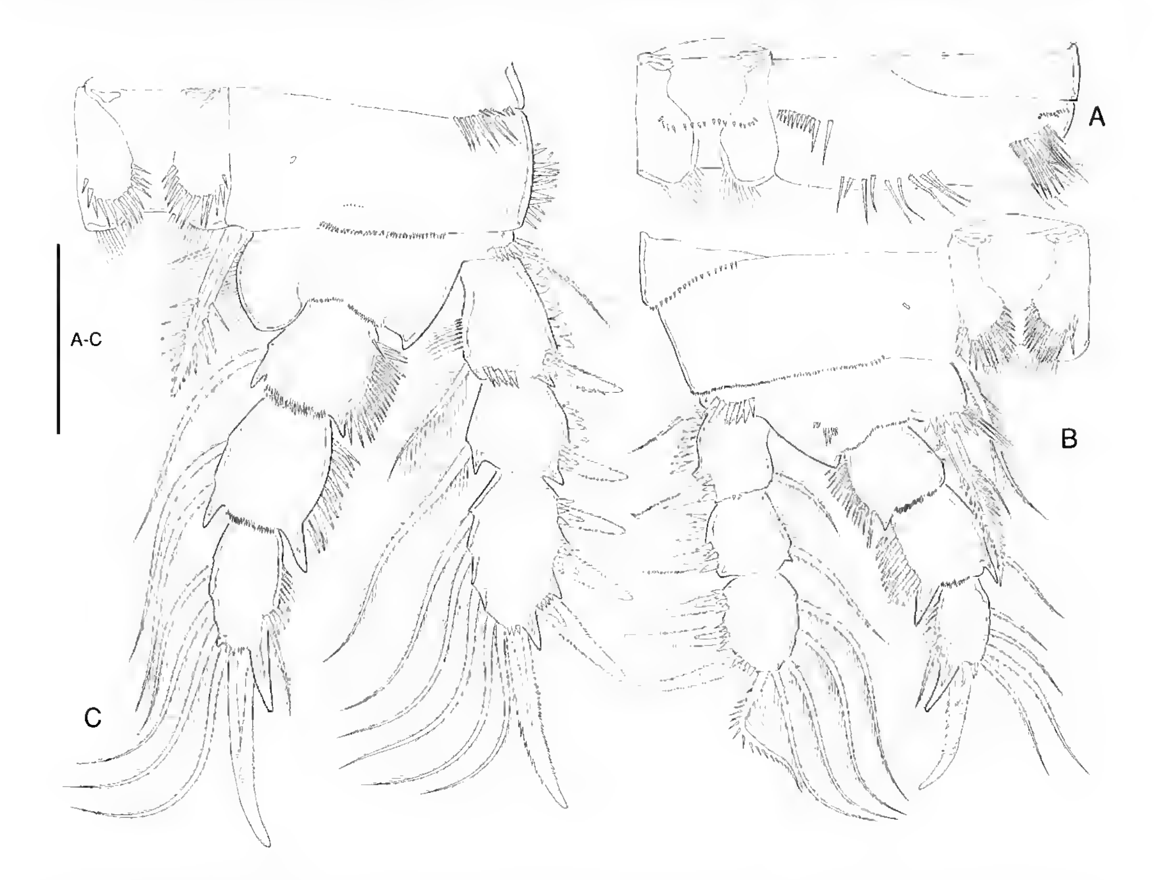


Fig. 20. — *P. chiltoni*; adult ♀; **A**, intercoxal sclerite and coxa of leg 1, posterior; **B**, leg 1, anterior; **C**, leg 2, anterior. Scale bar: 50 µm.

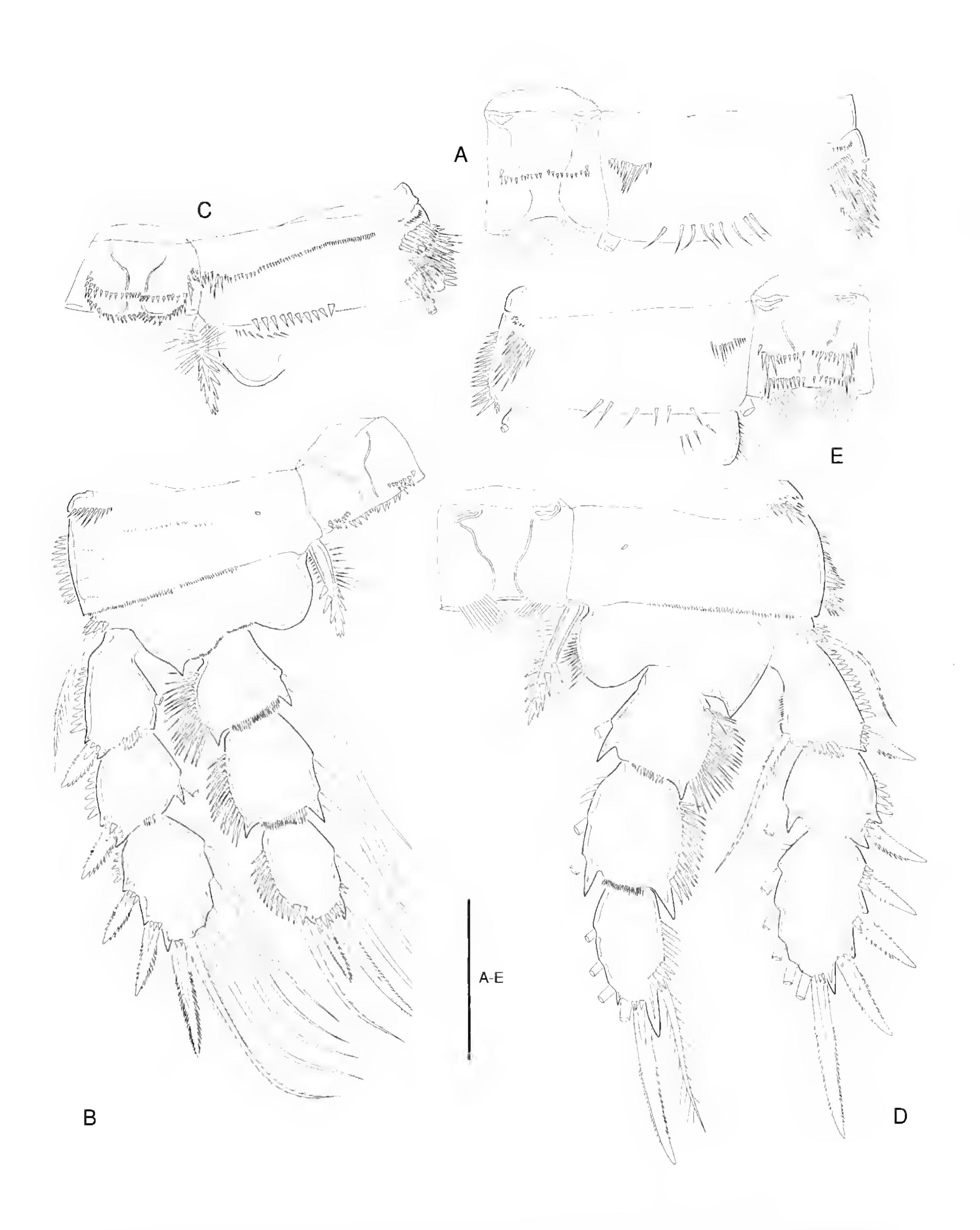


FIG. 21. — *P. chiltoni*; adult ♀; **A**, intercoxal sclerite and coxa of leg 2, posterior; **B**, leg 4, anterior; **C**, intercoxal sclerite and coxa of leg 4, posterior; **D**, leg 3, anterior; **E**, intercoxal sclerite and coxa of leg 3, posterior. Scale bar: 50 µm.

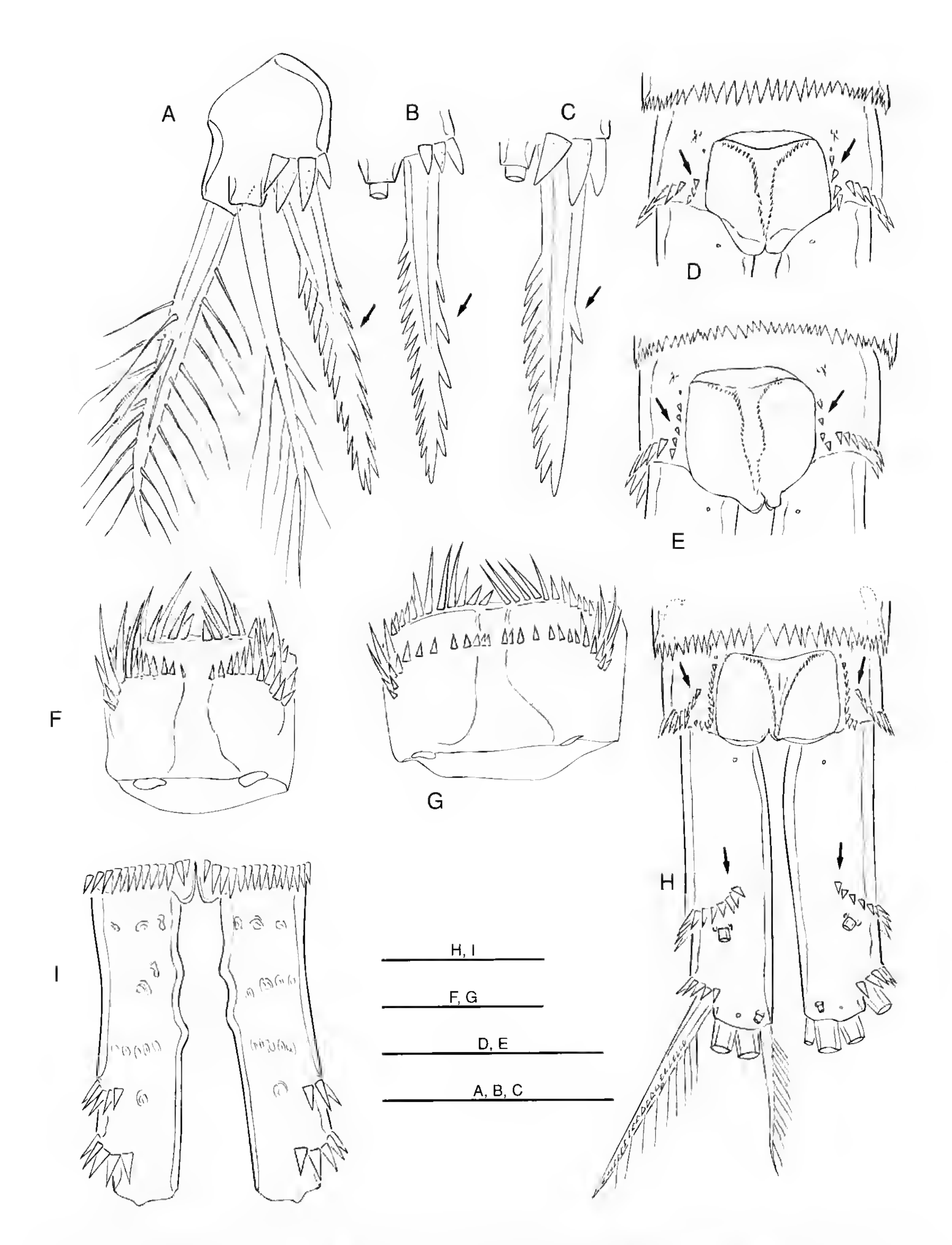


FIG. 22. — *P. chiltoni*; **A** (New Zealand), adult ♀, leg 5, ventral; **B** (U.K.), **C** (Brazil), adult ♀, inner spine of leg 5, ventral; **D**, adult ♂, **E**, adult ♀, anal somite, dorsal (Tahiti); **F**, adult ♂; **G**, adult ♀, leg 4, intercoxal sclerite, posterior (Brazil); **H**, adult ♀, anal somite and caudal rami, dorsal (Brazil); **I**, adult ♀, caudal rami, ventral (St Petersburg). Scale bars: A-C, F, G, 25 µm; D, E, H, I, 50 µm.

inner spine of leg 5 was slightly different in some specimens from England (Fig. 22B) and from the State of São Paulo, Brazil (Fig. 22C). In material from Tahiti, the number of spinules in the anal cleft, either side of the midline (arrowed in Fig. 22D, E), was very small in both sexes. In specimens from the State of São Paulo, Brazil (Fig. 22H) with relatively longer caudal rami, the terminal accessory seta (VI) is shorter than the posterolateral seta (III), and the spinular row at the base of the anterolateral seta (II) is slightly curved anteriorly (arrowed in Fig. 22H). In some specimens from New Zealand, England and Russia (St Petersburg), the inner margins of the caudal rami may be irregular, not smooth (Fig. 22I). The distal spinules on the posterior surface of the intercoxal sclerite of leg 4 are especially well-developed in females from the State of Rio Grande in Brazil (Fig. 22G) and in males from the State of São Paulo in Brazil (Fig. 22F).

Differential diagnosis

P. chiltoni can be differentiated from other *Paracyclops* species by the combination of the following four characters: (1) the structure of leg 5 (Figs 18C, 22A); (2) the presence of the conspicuous, well-developed spinular row near the base of two setae on the coxobasis of antenna in the male (arrowed in Fig. 23E), this spinular row is not present in the female (arrowed in Fig. 19B); (3) the obvious, dense, cuticular ornamentation of pits on the dorsal and ventral surfaces of the genital double-somite, and second and third urosomal somites (Fig. 18A); (4) the presence of similar cuticular depressions on the ventral surface of the caudal rami (Fig. 18B). The last character may be less pronounced in some specimens from outside the Palearctic region and should therefore be used with caution.

P. chiltoni also differs from *P. fimbriatus* and *P. imminuta* in the much shorter outer seta of leg 5 (Figs 18C). In the male of *P. chiltoni*, aesthetasc G on the first antennulary segment is present (Fig. 18D) but this aesthetasc is absent in *P. fimbriatus*.

Remarks

Paracyclops chiltoni (Thomson, 1882) was originally described from New Zealand. Later, Kiefer (1928) described *P. finitimus*, which matches well with *P. chiltoni* described herein, on the basis of the very short caudal rami, only three times as long as broad, and the short outer seta of leg 5 which is about as long as the inner spine. Kiefer (1931) expressed the opinion that Thomson (1882) likewise had found *P. finitimus* and therefore synonymized *P. chiltoni* with *P. finitimus*. However, according to the rules of Zoological Nomenclature, *P. chiltoni* takes priority and consequently *P. finitimus* is here ranked as a junior subjective synonym of *P. chiltoni*. Dussart & Defaye (1985) had earlier accepted *P. finitimus* as a synonym of *P. f. chiltoni*.

DISCUSSION

Currently, seven species of *Paracyclops* occur in the Palearctic region of which *P. baicalensis*, *P. dilatatus*, *P. affinis* and *P. poppei* are each quite distinct in their morphology (Karaytug 1998). *P. fimbriatus*, *P. imminuta* and *P. chiltoni* are, however, very closely related and the failure to separate *P. imminuta* from the other two of the species complex was the main reason behind the taxonomic confusion concerning all three. This taxonomic problem could not have been solved by using traditional features such as proportional measurements of the caudal rami and the terminal spines of the third endopodal segment of leg 4, because these characters vary considerably within populations as well as between populations. Since there is extensive overlap in variability expressed between these three variable species, it is concluded that most early records are unreliable.

The type material of none of the three species is extant. In the absence of types it was concluded that the best option would be to redescribe *P. fimbriatus* from the vicinity of St Petersburg, one of the listed type localities, on the basis of newly collected topotypic material. Examination of three unsorted samples from the vicinity of St Petersburg revealed four distinct *Paracyclops* species, *P. fimbriatus*, *P. poppei*, *P. chiltoni* and *P. imminuta*. It is interesting to note that the sample from P. Dudergofka (St Petersburg)

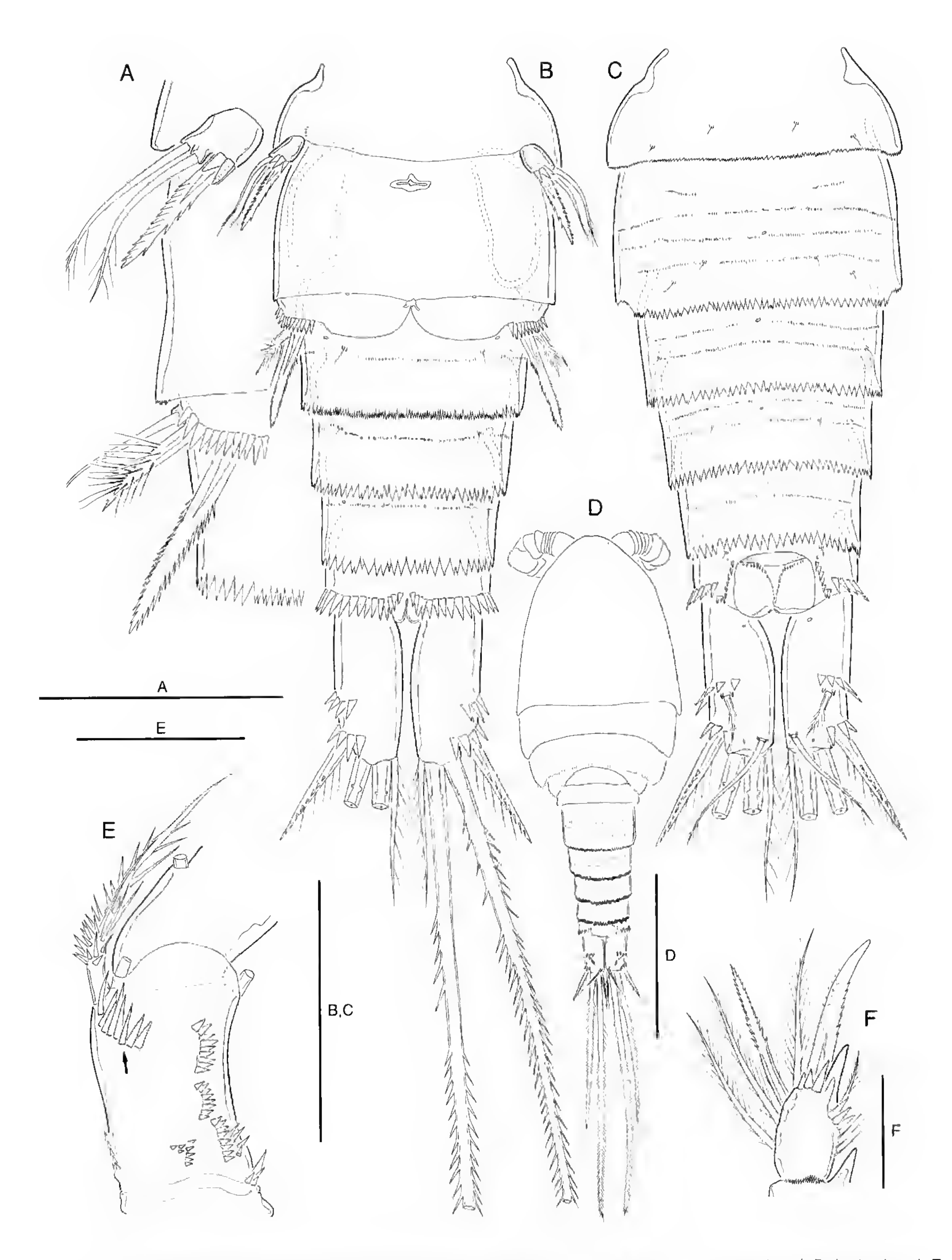


FIG. 23. — *P. chiltoni*, adult ♂; **A**, detail of leg 5 and leg 6, ventral; **B**, urosome, ventral; **C**, urosome, dorsal; **D**, body, dorsal; **E**, antenna, coxobasis, caudal; **F**, terminal endopodal segment of leg 1. Scale bars: A, 50 µm; B, C, 100 µm; D, E, F, 25 µm.

contained four females of *P. fimbriatus*, one female of *P. imminuta*, and four females of *P. chiltoni*. The sample from the River Igora (St Petersburg) contained fourteen females of *P. fimbriatus* and one female of *P. imminuta*. The sample from River Ravan (St Petersburg) contained two females of *P. fimbriatus* and seven females, three males of *P. poppei*. A single female of *P. fimbriatus* from R. Dudergofka (St Petersburg, Russia) was selected as the neotype.

Detailed redescriptions of *P. chiltoni* and *P. poppei* left no doubt that they are distinct species. The fourth taxon present in the St Petersburg samples was very problematic. It closely resembled the rather variable *P. fimbriatus* but could be distinguished on the basis of the arrangement of spinular row on the posterior surface of coxa of leg 1 and the presence of the spinular row near the base of two inner setae on the coxobasis of antenna.

Historically there have been some questions concerning the validity of several of the named species and subspecies of the *Paracyclops fimbriatus* complex. Gurney (1933) expressed certain doubts about the validity of *P. abnobensis* Kiefer, 1929 and *P. finitimus* Kiefer, 1928. Rylov (1963) agreed with Gurney's doubts and treated these two nominal species as varieties of *P. fimbriatus*. Lindberg (1958) synonymized *P. fimbriatus* forma *imminuta* Kiefer, 1929 with *P. fimbriatus chiltoni* which he accepted as a valid subspecies. Lindberg (1958) also synonymized the previously described species and subspecies on the basis of similarities between old descriptions, apparently without comparing type material and without giving detailed redescriptions.

Few workers have considered the possibility that the underlying reason for the gross variability found in particular populations of *P. fimbriatus* is the co-existence of closely related sympatric species. A first indication was given by Frenzel (1976) who studied a number of populations of *P. fimbriatus* from locations in Germany and Tenerife in which both "typical" and "*chiltoni*-type" specimens co-occurred. Using the "Furcal index" [Length (L): Width (W) ratio of the caudal rami in which W is measured halfway L] he recognized a distinct discontinuity separating two groups which were also distinguished – be it to a lesser extent – on the basis of the distance measured proximally between both caudal rami. Frenzel (1976) remarked that the P5 was remarkably constant in the group with short caudal rami and agreed in form and shape with Lindberg's (1958) illustrations of *P. fimbriatus chiltoni*. Because both groups still showed overlap in several other morphometric parameters, Frenzel (1976) left the matter undecided and concluded that only breeding experiments or more sophisticated techniques such as chromosome research could elucidate the problem. In a later paper Frenzel (1977) conducted various breeding experiments and succeeded in proving that at least three reproductive isolates ("Kreuzungsisolate") occurred in his samples, of which two could be identified with already described species, i.e. *P. fimbriatus* and *P. chiltoni*. The author also found that for each of these the morphometry of the caudal rami and the morphology of the P5 remained largely constant during successive generations and temperature did not seem to have any significant influence on these characters. All three had the same chromosome number in the female (2n = 13) which is identical to that found in *P. affinis* (Braun, 1909). It has to be remarked here that Frenzel did not study any possible differences in chromosome structure. Frenzel (1977) concluded that although the three types were entirely intersterile, clearcut distinction on purely morphological grounds was as yet impossible since an intermediate form was also separated during the breeding experiments. He recommended further cross-breeding experiments with other species such as *P. abnobensis*, *P. poppei* and *P. andinus* in order to test the distinctiveness of the three German types. In the absence of type material, it was impossible to assign Fischer's (1853) *Cyclops fimbriatus* to either *P. fimbriatus* or *P. imminuta* or even to *P. chiltoni*. The two critical characters that best separate *P. fimbriatus* from the other two species cannot be discerned from Fischer's original drawings. These characters are:

1. The spinular ornamentation on the frontal surface of the coxobasis of the antenna of both sexes.

2. The pattern of spinular ornamentation on the posterior surface of the coxa of leg 1.

The shape and length-width ratio of the caudal ramus of *P. fimbriatus* and *P. imminuta* as well as their geographical distributions overlap to a certain extent. Unfortunately, Fischer's original drawings of caudal rami fall within that degree of overlap. For the sake of nomenclatural stability the species that has been believed to be true *Paracyclops fimbriatus* by the majority of workers dealing with Palaearctic material, which occurs in St Petersburg and which could be represented by Fischer's figures, has been chosen here for redescription as typical *P. fimbriatus*.

The morphology of *P. fimbriatus* from Asia differs slightly from that of European specimens. Some variation is noted in the arrangement and number of spinular rows on the posterior surface of the intercoxal sclerite of leg 4 as well as in the shape of the inner coxal spine (slightly curved) on leg 4 in some specimens from the vicinity of Lake Baikal (Fig. 6H, I), Mongolia, Uzbekistan and India (Fig. 6G, K). Material from India especially showed remarkable variability on the inner spine of leg 5 as shown in figure 6A-C. The inner spine was usually longer than in other material examined and spinules were present at the base of the middle seta in some specimens (Fig. 6B, C). It is possible that Asian specimens of *P. fimbriatus* tend to show a greater degree of variability in these characters. Examination of more *P. fimbriatus* material from Asia, and the opportunity to carry out breeding experiments between them, would provide valuable new information on the taxonomy of *P. fimbriatus* in this part of the Palaearctic.

P. fimbriatus and *P. imminuta* are, at present, distributed probably throughout the Palaearctic. However, the biogeography of *P. chiltoni* is remarkable because it is the only species of the genus with very wide distribution (Karaytug 1998). It occurs, for example, in very remote locations, such as Easter Island, as well as in Europe. Breeding experiments between geographically isolated populations would provide new insights into the possible involvement of several sibling species of *P. chiltoni*.

Acknowledgements

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A second species of the genus *Balssia* Kemp, 1922 (Crustacea, Decapoda, Pontoniinae)

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Bruce A. J. 1998. — A second species of the genus *Balssia* Kemp, 1922 (Crustacea, Decapoda, Pontoniinae). *Zoosystema* 20 (4): 603-611.

KEY WORDS
Balssia noeli,
Crustacea,
Decapoda,
Pontoniinae,
new species,
Mediterranean Sea,
taxonomy,
commensalism.

ABSTRACT
A new species of commensal pontoniine shrimp, *Balssia noeli* n.sp., from the vicinity of Banyuls, western Mediterranean, is described and illustrated. The new species is readily distinguished from *B. gasti* (Balss, 1921), the only other species of the genus, by its lack of strong sculpturing on the carapace and abdomen. The species is associated with the gorgonians *Corallium*, *Eunicella*, *Gerardia* and *Paramuricella*.

MOTS CLÉS
Balssia noeli,
Crustacea,
Decapoda,
Pontoniinae,
espèce nouvelle,
Méditerranée,
systématique,
commensalisme.

RÉSUMÉ
Une deuxième espèce du genre Balssia *Kemp, 1922 (Crustacea, Decapoda, Pontoniinae).* Une nouvelle espèce de crevette pontoniine, *Balssia noeli* n.sp., provenant de la région de Banyuls, Méditerranée occidentale, est décrite et illusrrée. La nouvelle espèce se distingue facilemenr de *B. gasti*, la seule autre espèce du genre, par la sculpture beaucoup moins accentuée de la carapace et de l'abdomen. L'espèce est associée aux gorgones *Corallium*, *Eunicella*, *Gerardia* et *Paramuricella*.

INTRODUCTION

A single specimen of *Amphipalaemon gasti*, a small shrimp associated with the precious coral, *Corallium rubrum* (Linnaeus, 1758) from the Gulf of Naples, was first described and illustrated by Heinrich Balss in 1921. Kemp (1922) recognized that the species was a pontoniine shrimp and did not belong in the genus *Amphipalaemon* Nobili, 1901, now considered a synonym of the genus *Anchistioides* Paulson, 1875 in the family Anchistioididae. The new genus *Balssia* was then designated for its reception. The species has since been reported from a wide range of localities on the European coasts of the western Mediterranean and Adriatic Seas, Corsica, the Canary Islands and some West African localities, and from a variety of host animals (Manconi & Mori 1990). The discovery of a second species in the western Mediterranean suggesrs that some of the earlier records should be re-examined ro confirm that they do all refer to *Balssia gasti* (Balss, 1921). The specimens are deposited in the collection of the Muséum national d'Histoire naturelle, Paris (MNHN), Nationaal Natuurhistorisch Museum, Leiden (NNM), and Queensland Museum, Brisbane (QM).

I am most grateful to Dr Pierre Noël for the opportunity to report upon these specimens.

Carapace length (CL) refers to the post orbital carapace length.

SYSTEMATICS

Family PALAEMONIDAE Rafinesque, 1815
Subfamily PONTONIINAE Kingsley, 1878
Genus *Balssia* Kemp, 1922

Balssia noeli n.sp.
(Figs 1-4)

Balssia sp. – Noël 1992: 64.

MATERIAL EXAMINED. — **Mediterranean Sea.** Vicinity of Banyuls: 7 ovigerous ♀♀, 1 ovigerous ♀, 1 ovigerous ♀ (Laboratoire Arago).
From "ancient collections", details of exact localities, dates, depths and collectors not available.

TYPES. — The ovigerous female holotype is deposited in the collection of the Muséum national d'Histoire naturelle, Paris, catalogue number MNHN-Na 13440, together with the dissected pararype female, MNHN-Na 13441. A paratype is also deposited in the collection of the Nationaal Natuurhistorisch Museum, Leiden, catalogue number RMNH D 47887, and one in the Queensland Museum, Brisbane, number QM W 23107. The remaining specimens are also designated as paratypes.

MEASUREMENTS. — Ovigerous female holotype, carapace length 4.0 mm; carapace and rostrum 6.0 mm; total body length (approx.) 15.5 mm; second pereiopods, major chela 1.6 mm; minor chela 1.6 mm; length of ovum 0.5 mm.

COLORATION AND HOSTS. — The specimens, all from gorgonacean coelenterates, were annotated as follows: from lot #1, (1) white, on *Eunicella* Verrill, 1869; (2) violet, on *Paramuricella* Kölliker, 1865; (3) yellow, on *Gerardia* Lacaze-Dultriers, 1864 (zoantharian of the family Parazoanthidae); (4) red, on *Corallium* Cuvier, 1826. No data available on colouration or hosts of lots #2-#3.

ETYMOLOGY. — The species is named in honour of Dr. Pierre Y. Noël, who kindly provided the specimens upon which this report is based.

DESCRIPTION (ovigerous females, Fig. 1)
Small stoutly built pontoniine shrimps of generally subcylindrical body form (Fig. 1), cephalothoracic region ventrally flattened.

Rostrum (Fig. 2A, C)
Slender, oval in section, without distinct carinae, about 0.5 of carapace length, reaching to end of intermediate segment or middle of distal segment of antennular peduncle, distally acute, with three small acute reeth dorsally, proximal teeth large, acute, distal tooth small, ventrally unarmed, few median setae proximally only.

Carapace (Fig. 2A)
Swollen, globular, smooth, cervical groove feebly indicated, small cervical and hepatic tubercles usually discernible, with distinct postrostral carina bearing two small teeth, posterior tooth usually obruse, anterior rooth acute, small epigastric tooth present or absent; orbit well-developed, superior margin carinate with three small acute teeth, posrerior margin incomplete, lateral border carinate with two subacute tubercles posteriorly,

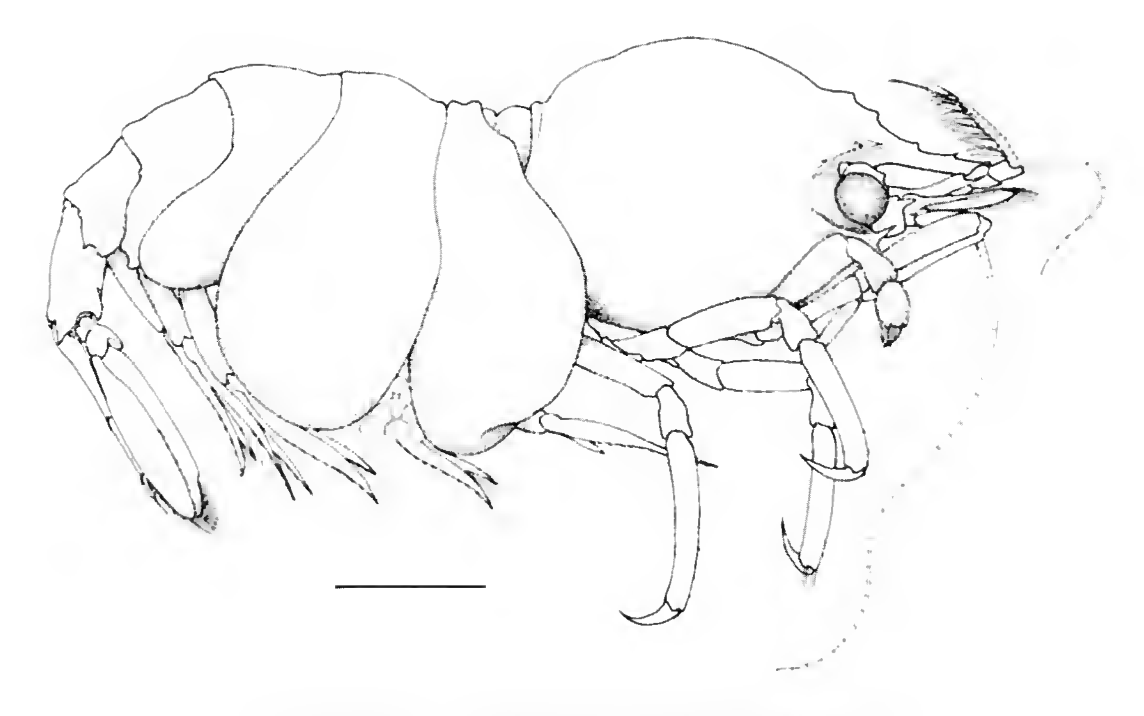


FIG. 1. — *Balssia noeli* n.sp., ovigerous holotype ♀. Banyuls. Scale bar: 2.0 mm.

continuous with large acute dorsolaterally angled antennal spine, branchio-stegal sulcus present below lateral orbital margin, anterolateral margin of branchiostergite slightly produced, rounded, inferior orbital angle broadly triangular.

Abdominal segments (Fig. 2E, I, 4K)
Smooth, third segment not posteriorly produced, non-carinate, first three pleura expanded, broadly rounded, fourth with posterior margin feebly bilobed, centrally feebly carinate laterally, fifth similar with upper lobe acutely produced, sixth segment 1.6 times length of fifth, 2.0 times longer than central depth, posterolateral angle strongly produced, acute, posteroventral angle produced, subacute.

Telson (Fig. 2I)
About 1.8 times length of sixth segment, about 3.0 times longer than anterior width, lateral margins straight, posteriorly convergent, with small subequal marginal lateral spines at 0.5 and 0.9 of telson length, posterior margin (Fig. 4K) 0.3 of anterior width, transversely truncate, without median point, lateral posterior spines similar to dorsal spines, intermediate spines about 0.75 of telson length, about 7.5 times longer than basal width, submedian spines slender, setulose, shorter than intermediate spines.
Ophthalmic somite dorsally antero-posteriorly bilobed, without pigment spot.

Antennular peduncle (Fig. 2G)
Normal, with short flagella; proximal segment 1.2 times longer than broad, lateral margin expanded, angular, produced distally with small rounded lobe reaching to middle of intermediate segment length, with large acute slender distolateral tooth, exceeding intermediate segment length, ventromedial margin with strong tooth at 0.5 of length, intermediate and distal segments normal, subequal, combined length about 0.7 of proximal segment length, intermediate segment with small setose lateral lobe, upper flagellum biramous with eight proximal segments fused, shorter free ramus with four segments, with about eighteen groups of aesthetascs, lower ramus short, filiform.

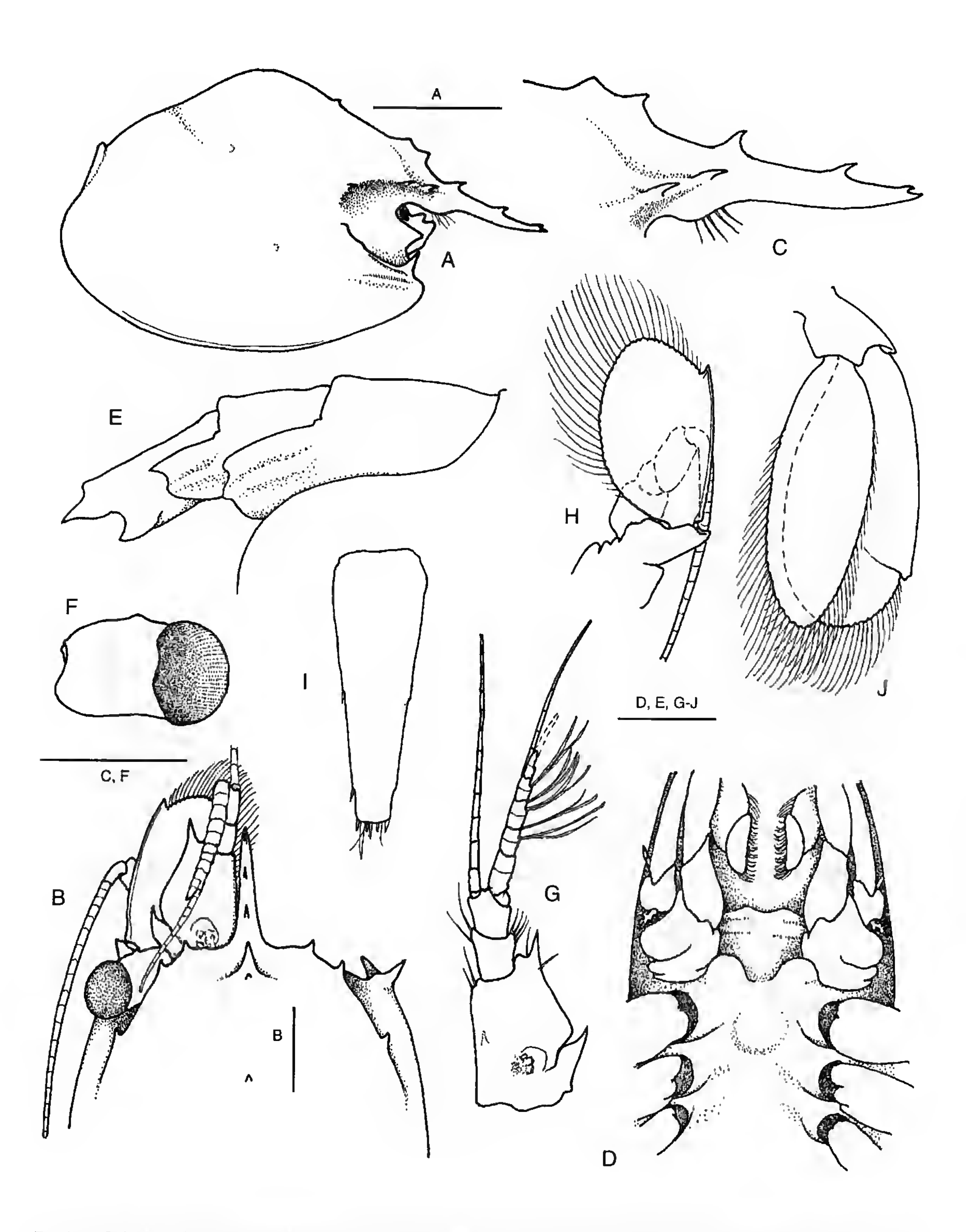


FIG. 2. — *Balssia noeli* n.sp., paratype ovigerous ♀, Banyuls; **A**, carapace and rostrum; **B**, anterior carapace and left appendages, dorsal; **C**, rostrum; **D**, thoracic sternites, ventral; **E**, fourth to sixth abdominal segments, lateral; **F**, eye, dorsal; **G**, antennule; **H**, antenna; **I**, telson; **J**, uropod. Scale bars: A, 2.0 mm; B-J, 1.0 mm.

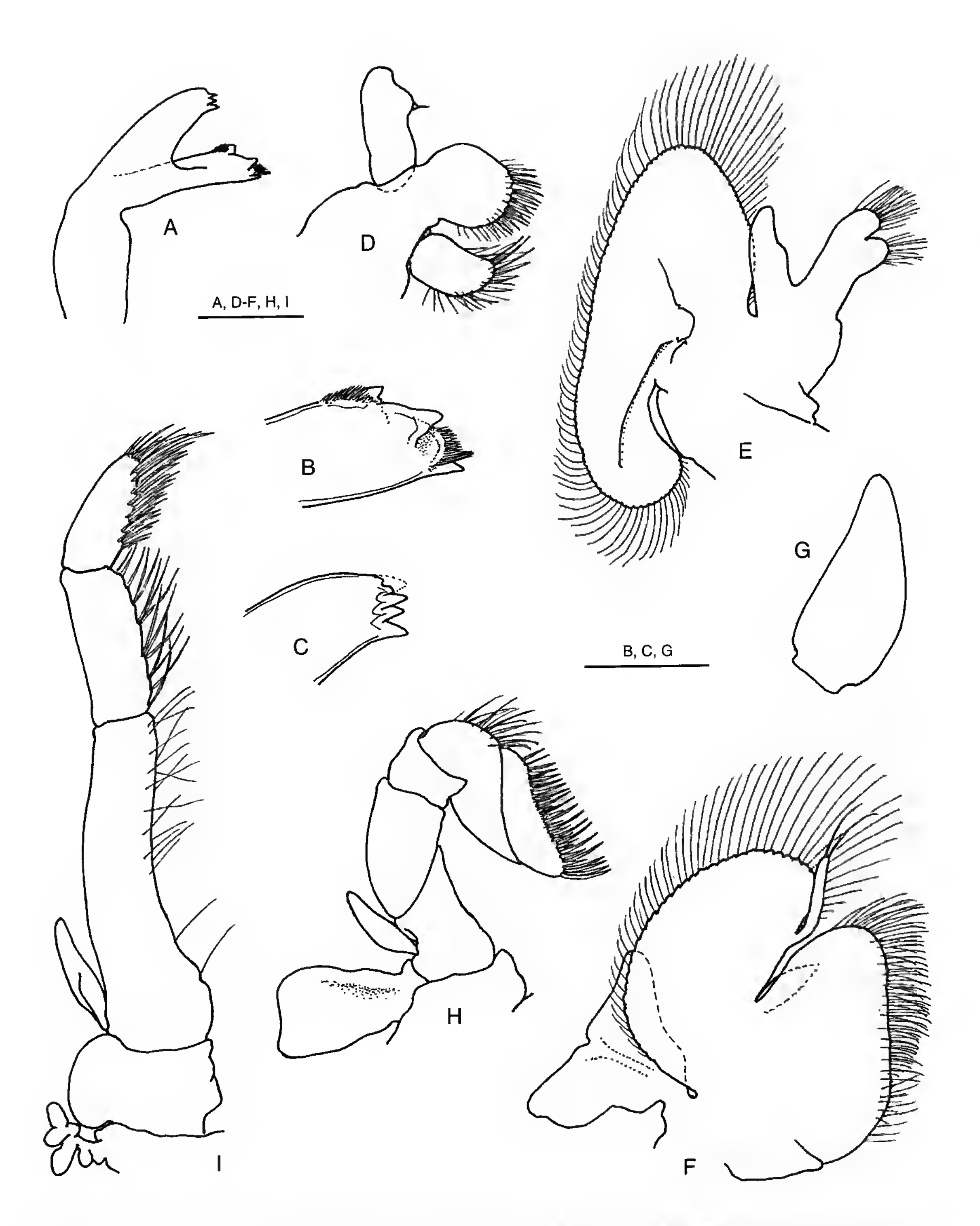


FIG. 3. — *Balssia noeli* n.sp., paratype ovigerous ♀, Banyuls, mouthparts; **A**, mandible; **B**, mandible, molar process; **C**, mandible, incisor process; **D**, maxillula; **E**, maxilla; **F**, first maxilliped; **G**, first maxilliped, palp; **H**, second maxilliped; **I**, third maxilliped. Scale bars: A, D-F, H, I, 0.5 mm; B, C, G, 0.2 mm.

Antenna (Fig. 2H)
With basicerite stout, with small blunt antero-lateral tooth; carpocerite short stout, reaching to about half scaphocerite length, flattened, about 2.0 times longer than wide, flagellum short, about 2.0 times carapace length; scaphocerite broad, about 1.6 times longer than central width, lateral margin feebly convex, with small acute distal tooth, at about 0.8 of lamellar length, falling far short of anterior margin of lamella.

Eye (Fig. 2F)
Stout, with well-pigmented globular cornea, diameter about 0.18 of carapace length, without accessory pigment spot, stalk length subequal to width and corneal diameter, with minute antero-dorsal tubercle.

Mouth parts
Mandible (Fig. 3) slender, without palp; incisor process (Fig. 3C) slender, tapering, with four small acute teeth distally, central pair smaller than outer teeth; molar process (Fig. 3B) slender, obliquely truncate distally, with three small stout, blunt teeth and two bands of setae. Maxillula (Fig. 3D) with feebly bilobed palp, lower lobe with single short seta; upper lacinia short, subcircular, with several short simple spines distally and numerous finely serrulate setae; lower lobe short and broad, with numerous spiniform setae distally and ventrally. Maxilla (Fig. 3E) with short broad, non-setose palp, medial margin sinuous, distal endite feebly bilobed, lobes subequal, upper lobe with about fifteen slender simple setae, lower lobe with about ten, proximal endite obsolete, medial margin feebly convex; scaphognathite broad, about 3.4 times longer than central width. First maxilliped (Fig. 3F) with short, non-setose, tapering palp (Fig. 3G), about 2.3 times longer than proximal width, basal and coxal endites completely fused, broad, about 1.9 times longer than wide, broadly rounded distally, medial margin distally straight, proximally concave, fringes with numerous slender, feebly serrulate setae; exopod with flagellum greatly reduced, scarcely exceeding caridean lobe, subcylindrical, with two short plumose setae distally, caridean lobe large, broadly expanded, 2.0 times longer than broad; epipod large, triangular, feebly bilobed. Second maxilliped (Fig. 3H) with endopod of normal form, dactylar segment narrow, medial margin with numerous long serrulate spines, propodal segment not antero-medially produced, ischiomerus and basis normal, with exopod greatly reduced, not exceeding basis, lamellar, non-setose; coxa stout, without medial process, epipod well-developed, triquetral, without podobranch. Third maxilliped (Fig. 3I) reaching to about middle of carpocerite length, ischiomerus and basis completely fused, junction indicated by small medial margin notch, about 3.0 times longer than proximal width, tapering distally, sparsely setose alone distal medial margin, penultimate segment about 0.5 of ischiomerus-basal segment, 2.3 times longer than central width, uniform, with numerous serrulate spiniform setae medially, distal segment about 0.4 of ischiomeral-basal segment length, 2.4 times longer than proximal width, densely spinulose medially and distally, with serrulate spines; exopod as in second maxilliped; coxa with small non-setose medial process, broad rounded lateral plate and rudimentary arthrobranch present.

Thoracic sternites (Fig. 2D)
Broad, first with small transverse, feebly bilobed carina, third widest (so that third maxillipeds are lateral to first pereiopods in ventral view), fourth without median process, with rounded lateral lobes, posterior sternites broad, without special features.

First pereiopods (Fig. 4A, B)
Slender, exceeding carpocerite by chela and carpus, chela (Fig. 4B) slender, palm subcylindrical, tapering slightly distally, about 3.6 times longer than wide, fingers about 0.66 of palm length, slender, with simple acute tips, cutting edges entire, lateral; carpus about 1.25 times longer than chela, 6.5 times longer than distal width, subcylindrical, tapering slightly proximally; merus about 0.9 of carpus length, of similar width, ischium about 0.9 of chela length, basis and coxa normal, coxa with small setose ventro-medial process.

Second pereiopods (Fig. 4C-G)
Feebly developed, subequal, similar; exceeding

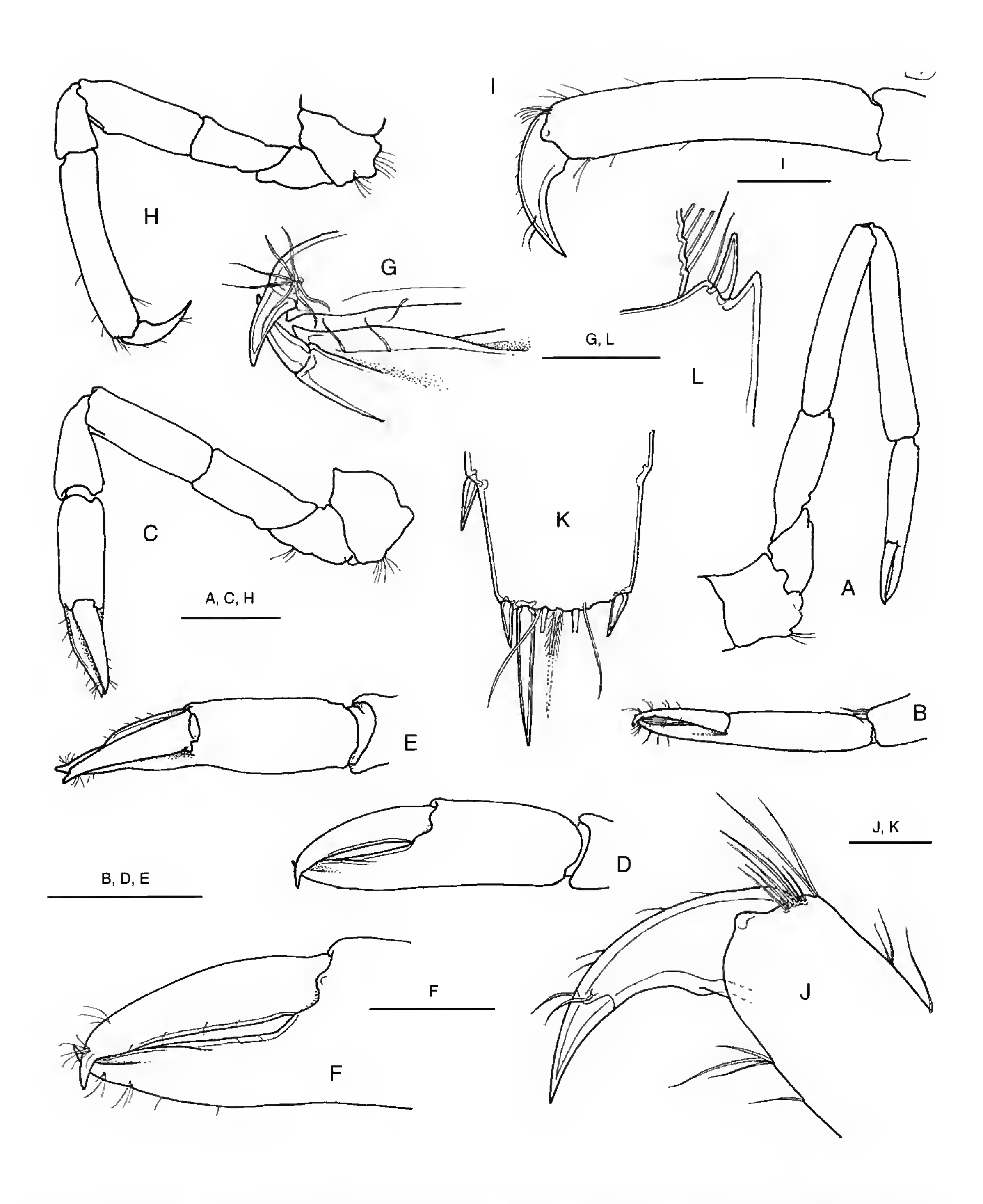


FIG. 4. — *Balssia noeli* n.sp., paratype ovigerous ♀, Banyuls; **A**, first pereiopod; **B**, first pereiopod, chela; **C**, second pereiopod; **D**, second pereiopod, chela, medial; **E**, second pereiopod, dorsal; **F**, second pereiopod, fingers; **G**, second pereiopod, finger tips; **H**, third pereiopod; **I**, third pereiopod, propod and dactyl; **J**, third pereiopod, distal propod and dactyl; **K**, telson, posterior margin; **L**, uropod, posterolateral angle of exopod. Scale bars: A-E, H, 1.0 mm; F, I, 0.5 mm; G, J-L, 0.2 mm.

carpocerite by length of fingers; chela (Fig. 4D, E) about 0.4 of carapace length, palm smooth, oval in section, about 1.8 times longer than distal depth, fingers (Fig. 4F) subequal to palm length, sparsely setose, gaping slightly proximally, dactylus slender, curved, slightly compressed, tip (Fig. 4G) with stout acute articulated tooth with small, non-articulated tooth laterally, cutting edge lateral, entire, fixed finger similar but expanded proximally, cutting edge present distally, entire; carpus short, stout, unarmed, 2.0 times longer than distal width, tapered proximally, subequal to palm length; merus 1.2 times palm length, about 3.0 times longer than wide, uniform, unarmed; ischium subequal to palm length, unarmed, basis and coxa normal, without special features.

Ambulatory pereiopods (4H-J)
Robust, third (Fig. 4H) exceeding carpocerite by length of dactylus, dactylus (Fig. 4J) about 0.45 of propod length, stout, simple, acute, strongly curved, with feebly demarcated unguis, about 0.5 of corpus length, 3.0 times longer than basal width, corpus compressed, dorsal margin convex, 2.0 times basal depth, with paired sensory setae distally, sparse setae along dorsal margin; propod (Fig. 4I) about 0.4 of carapace length, 6.0 times longer than depth, uniform, slightly bowed, without spines, sparse setae distally, carpus about 0.3 of propod length, 1.6 times longer than distal width, tapering proximally, unarmed, merus 0.65 of propod length, 2.6 times longer than deep, unarmed, ischium 0.5 of propod length, unarmed, basis and coxa normal, without special features, coxa stout. Fourth and fifth pereiopods similar, fourth with propod 0.8 of third propod length, fifth subequal to third.

Uropod (Fig. 2J, 4L)
With protopodite with small blunt posterolateral lobe; exopod broad, about 2.1 times longer than wide, lateral margin convex, unarmed, with small acute distal tooth (Fig. 4L) with larger mobile spinule medially; endopod reaching to distal end of exopod, about 2.8 times longer than wide.

Ova very numerous, small.

Systematic position
A well-illustrated account of *Balssia gasti* was provided by Balss (1921), based on a single ovigerous female specimen, and is therefore fully comparable with the present material. Manconi & Mori (1990) state that, in *B. gasti*, the carapace length ranges from 3.2 to 4.0 mm in ovigerous females so that the two species are of similar size.
The major characters that distinguish *Balssia noeli* from *B. gasti* (Balss), the only other species of the genus, are as follows: shorter rostrum, not well exceeding antennular peduncle, with three smaller dorsal teeth only; a short bidentate post-rostral carina, with or without a small epigastric tooth; cervical and hepatic spines reduced to small tubercles; first three abdominal terga without median carinae; fourth pleuron lacking acute tooth posteriorly; anterodorsal eyestalk tubercle minute; anterolateral tooth of proximal segment of antennular peduncle not well exceeding intermediate segment; maxilla with distal endite feebly bilobed; fixed finger of second pereiopod with proximal half only expanded.

Remarks
In the original description of *Balssia gasti*, Balss noted particularly the strong sculpturing, of the carapace, and abdomen, with a distinct dorsal carina the absence of which most clearly separates his species from *B. noeli*. It is possible that the as yet unknown males of *B. noeli* will show a more strongly sculptured appearance than the females, as is known to occur in some other ornate pontoniine associates of coelenterates such as *Dasycaris zanzibarica* (Bruce, 1973). The differences are not strongly marked in *B. gasti* as is shown by the figures in Zariquiey Alvarez (1946, fig. 111).
Balssia gasti was first found in association with the precious coral *Corallium rubrum* (L., 1758), an alcyonacean host. Most subsequent records have been from this host. There have also been a number of records from other hosts, reviewed by Manconi & Mori (1990), including several from gorgonians, including species of *Eunicella*, *Gerardia*, *Lophogorgia* Milne Edwards, 1857, and *Paramuricella*. Possibly some of these should be referred to *B. noeli*. Mori *et al.* (1994) have confirmed that their material, from Sardinia and associated with the gorgonian host *Paramuricella clavata* (Risso, 1826), belonged to Balss' species

sensu stricto, so there is no doubt that *B. gasti* can occur with both alcyonacean and gorgonian hosts. The associations reported with sponge hosts (Ledoyer 1968) seem likely to have been of accidental origin due to the exigencies of collection methods. However, the possibility of associations with sponges should be further investigated before its exclusion. The selection of host animals of *B. noeli* otherwise overlaps significantly with that of *B. gasti*, but further collections may show that each species has distinctive host preferences.

The specimen illustrated by Noël (1985) shows a marked absence of strong sculpturing on the carapace and may therefore belong to the present species. The live specimen was collected from Banyuls in the late 1960's or early 1970's by Alain Thiriot and photographed by Jean Lecomte. It was a pure yellow colour, associated with a gorgonian host, and may have formed part of the material upon which the present study is based (P. Y. Noël, pers. comm., January 1998).

The status of the various colour patterns and host animals remains mysterious. It is quite possible that colour pattern and host selection are genetically determined and that the various colour "forms" of each "species" actually represent a complex of related sibling species. Shrimp coloration may be under physiological control. There is ample scope for further study in these fields. Knowlton & Keller (1985), and Duffy (1996) have demonstrated that these complexes exist in some commensal Alpheidae and their occurrence in other caridean families seems highly likely. Some of the monospecific commensal shrimp genera that are found in association with a wide variety of different host types may well consist of several sibling species. Knowlton (1993) and Duffy (1996) consider that diversity in the relevant taxa is probably several times greater than presently recognized and that this is correlated with a high degree of host specificity.

Acknowledgements

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Evolution of the abdominal holding systems of brachyuran crabs (Crustacea, Decapoda, Brachyura)

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ABSTRACT
Brachyuran decapod crustaceans are characterized by a reduced abdomen, folded beneath the cephalothorax, and inserted between the pereiopods or in a special cavity, which prevents it from impeding movements. The acquisition of a retaining/locking mechanism may be regarded as a synapomorphy for the Brachyura. In primitive podotrematous forms (Dromiidae, Homolidae), the structures involve the coxae of thoracopods. In higher Brachyura, the structures located on limbs have moved onto the sternal plate. The most common holding system is the press-button, consisting of a prominence always on the fifth sternite and a socket always positioned on the sixth abdominal segment. The innovation with a sternal differentiation appears to have occurred independently several times: on sternite 4 (Homoloidea: homolid press-button), on sternite 5 (Dynomenidae, Lyreidinae), on sternite 6 (Phyllotymolinidae, Cyclodorippidae), and on sternite 5 (Eubrachyura: typical press-button). In the Heterotremata, only the Leucosiidae display a retaining system that differs from the typical press-button. A true socket evolved within the Podotremata (Homoloidea, Lyreidinae), and in almost all Eubrachyura. The abdominal socket is hypothesized to be homologous with the uropod. The absence of any locking structures in the most highly carcinized thoracotrematous crabs (for instance Ocypodinae *pro parte*) is considered to be the result of a secondary loss, occurring at about the time when terrestrial habitats replace the exclusively marine life. The microstructures, discovered on both homolid and typical press-buttons, might be regarded as an indicator of sex, puberty moult and age of individuals, and are probably reliable indicators of phylogenetic affinities at different levels.

KEY WORDS
Abdomen,
Brachyura,
coaptation,
holding system,
homology,
locking mechanism,
microstructure,
press-button,
phylogeny,
uropod.

RÉSUMÉ

Évolution des systèmes de maintien de l'abdomen chez les Brachyoures (Crustacea, Decapoda, Brachyura). Les Crustacés Décapodes Brachyoures sont caractérisés par un abdomen réduit, replié sous le céphalothorax et inséré entre les péréiopodes ou dans une cavité particulière, ce qui empêche toute gêne lors des déplacements. L'acquisition d'un système de maintien ou de fermeture de l'abdomen est considérée ici comme une synapomorphie des Brachyoures. Chez les formes primitives de Podotremata (Dromiidae, Homolidae) les structures font intervenir la coxa des thoracopodes. Chez les Brachyoures plus avancés les structures se trouvent déplacées sur le sternum thoracique. Le système le plus répandu est le bouton-pression, à savoir une proéminence appartenant toujours au sternite thoracique-5, et une fossette toujours située sur le segment abdominal 6. La novation que constitue la différenciation sternale serait apparue indépendamment plusieurs fois : sur le sternite 4 (Homoloidea : bouton-pression homolien), sur le sternite 5 (Dynomenidae, Lyreidinae), sur le sternite 6 (Phyllotymolinidae, Cyclodorippidae), et sur le sternite 5 (Eubrachyura : bouton-pression typique). Chez les Heterotremata, seuls les Leucosiidae offrent un système de maintien différent du bouton-pression typique. Une vraie fossette est apparue au sein des Podotremata chez les Homoloidea et les Lyreidinae, ainsi que pour l'ensemble des Eubrachyura. La fossette abdominale est ici homologuée à l'uropode. L'absence de structures chez les Thoracotremata les plus évolués (Ocypodinae *pro parte* par exemple) est considérée comme le résultat d'une perte, lors du passage d'un habitat exclusivement marin à un mode de vie amphibie. Les microstructures découvertes sur le bouton homolien et sur le bouton-pression typique représentent des indicateurs du sexe, de la mue de puberté et de l'âge des individus ; de plus, elles sont susceptibles de refléter les affinités phylogénétiques à divers niveaux.

MOTS CLÉS
Abdomen,
bouton-pression,
Brachyura,
coaptation,
homologie,
mécanisme d'accrochage,
microstructure,
phylogénie,
uropode.

INTRODUCTION

The term coaptation (from the Latin *cum*, with; *aptare*, fit), that for a long time referred to medical language for the setting of a fracture or luxation, was revived by the French biologist L. Cuénot (1921; 1925) to name, in arthropods and more especially in insects, the fitting between two different and originally independent parts of the body, with a more or less pronounced engagement.

Many types of coaptation are developed in almost all brachyuran crabs to retain their abdomen beneath the cephalothorax. The most well-known is the *bouton-pression* or press-button (Cuénot 1941). In the following scheme used in insects (Corset 1931), three main patterns, with several degrees of differentiation, may be recognized in the Brachyura, at the binocular level (Table 1, p. 634):

1. Coaptation by juxtaposition. There is a relative independence of both parts, a simple modality of union, or a simple joining: the two parts are only coupled. In the case when a spine or a projection simply overhangs or overlaps the other part, without inducing marked modifications, it may be considered the first state of a coaptation.

2. Coaptation by engagement (in French *engrenage*). Considered a more advanced degree: both corresponding parts are more differentiated but can be easily separated. A variety of configurations, from simple to more complex, exists.

3. Coaptation by assemblage (in French *assemblage*). One of the two parts, which were originally completely independent, is firmly engaged in a socket or a hollow, within which it is held

fast most of the time. The two parts can only be separated with difficulty and displaced in a given direction, often with a clicking sound. This is the case of the typical *bouton-pression* and homolid press-button.

In Brachyura the reduction-folding of the abdomen is probably the principal event in the process of carcinization, *i.e.* the adoption of a crab-like habitus. In contrast to long-bodied forms of decapods in which the developed and extended abdomen, with movable somites and large biramous pleopods, is used for locomotion, brachyuran crabs are characterized by a short abdomen that is basically formed by six segments plus the telson and lies in a flexed position. Brachyura lack locomotory appendages and tail fan, as they exist in "macruran" decapods for example: the locomotory function of the abdomen has been lost. Either the brachyuran abdomen is simply folded forward between the pereiopods, or it may be accommodated by a thoracic depression, the sterno-abdominal cavity, which is more or less hollowed and defined. Besides that, the pleon is secured in a flexed position and sometimes tightly held in place against the ventral surface by a special system.

In most primitive crabs the abdomen is simply held by the bases of various thoracopods (Mxp2, Mxp3, P1 through P3), and coaptations by juxtaposition and engagement are developed. But, in most crabs, the most common means consists of a "true" locking mechanism, the press-button. The press-button system is a coaptation by assemblage between structures that belong to two clearly defined somites of two different parts of the body: the fifth somite on the thoracic sternum and the sixth segment on the abdomen (or pleomere 6). It consists of a pair of salient structures on the sternal plate that fits into a pair of sockets on abdominal segment 6.

It is beyond the scope of this paper to reconstruct phylogenetic relationships within the Brachyura based on the abdominal holding apparatus. However, analysis of the different devices or strategies utilized by brachyuran crabs to retain or lock their abdomen sheds new light on the evolution of the group. In turn, using this criterion at different taxonomic levels might perhaps open a way for the reappraisal of the Brachyura.

MATERIALS AND METHODS

Our study is based on the large research collections of the Muséum national d'Histoire naturelle, which are essential for a sound, pragmatic basis for comprehensive analysis. The observations always involved dead specimens (alcohol preserved), that were often manipulated. That is why all our suggestions on the functioning must be reconsidered with fresh specimens and living animals. In the course of this work, thousands of specimens were investigated, but it is clear that our conclusions need to be completed and hypotheses are presented to serve as a basis for further investigations and discussion.

Representatives of several genera, belonging to fifty-seven families available to us, have been studied and illustrated. Some results are taken from the work in progress by one of us (J.-M. B.) on microstructures of the locking system with the scanning electron microscope.

We follow the classification of Guinot (1977, 1978a, *cf.* also Guinot & Richer de Forges 1997). The families, listed here in a certain order, do not represent a classification, even if a phylogenetic background is present. The list presented here is not exhaustive. Regarding the components of some families, the traditional arrangement was sometimes conveniently preferred; the family level was often preferred, because monophyly is better supported (but not in Varuninae for example). In any case we examined at least the type genus, and we attempted to extend our observations to all principal component genera. Our description essentially concerns the males since, generally, structures are lost in females after the puberty moult.

Carapace dimensions are given as carapace length followed by carapace width, the measures including any antero-lateral teeth at the widest point. cw, carapace width; cl, carapace length. Appendages and segments frequently referred to in descriptive accounts and figures are usually abbreviated as follows: P1-P5, pereiopods (P1, chelipeds, P2-P5, walking legs); Mxp1-Mxp3, maxillipeds; G1, first male pleopod; G2, second male pleopod. The term thoracopod is used for the appendages Mxp1-Mxp3 and P1-P5. We preferred the terminology somite 4 to fourth somite or

abdominal segment 4 to fourth abdominal segment, for example.

Abbreviations for the institutions are as follows:
BMNH The Natural History Museum, London;
MNHN Muséum national d'Histoire naturelle, Paris (MNHN-B used for catalogue number; B means Brachyura);
SAM South African Museum, Cape Town;
USNM National Museum of Natural History, Smithsonian Institution, Washington.

HISTORIC

The abdominal retaining apparatus, that is, a pair of sternal prominences and a pair of sockets on the penultimate segment of abdomen, was first reported and described by Duvernoy (1850) in a chapter on the external reproductive organs in the Decapoda. The first illustration was given in a second paper on the same subject by Duvernoy (1853), who wondered that such a "simple mechanism" (p. 141) was not previously observed. This author noticed its particular configuration in leucosiids and the loss of morphological structures in *Uca* Leach, 1814 (*Gelasimus* Latreille, 1817).
It took nearly 80 years to again hear about the abdominal retaining apparatus. Pérez (1928a, 1928b, 1929), another French scientist, created the term *bouton-pression* (an allusion to its function as a press-stud or a dome fastener) and reviewed the retaining structures in diverse Brachyura. He had a clear understanding about evolution of the system, regarding the dromiid disposition as basal, the system in *Homola* Leach, 1815 as intermediary (but not derived from *Dromia* Weber, 1795), the typical press-button present in the majority of crabs but finally lost in *Uca*, and the unusual arrangement in leucosiid forms. From this evolutionary scheme (1928b: 649) Pérez hypothesized that the border of the socket on pleomere 6 was perhaps the last vestige of the ancient uropod. Pérez (1933a, 1933b) examined the functional patterns with regard to sex, molt, and mating, and discussed the peculiar case of the feminization of the male abdomen in sacculinized *Pachygrapsus marmoratus* (Fabricius, 1787).
Dealing with the coaptations in Crustacea, Macquart (1936) briefly mentioned the locking mechanism in the Brachyura, suggesting that it may be replaced by another physiological system in advanced taxa such as *Uca*. Kollmann (1937) studied, with more detail, the coaptations between the abdomen and cephalothorax and the morphological parts involved in the retaining systems, following the configuration in primitive crabs such as *Dromia* and *Homola*, then in dorippids, in more advanced forms such as *Carcinus* Leach, 1814, *Maja* Lamarck, 1801, and in leucosiids. Cuénot (1935; 1941: 209-215, figs 43, 44) was interested by the problematics of coaptated organs and their finality: the brachyuran press-button was compared to systems found in the Cephalopoda and in hemipterid insects (Poisson 1922). But the typical locking mechanism device of brachyuran crabs was only noticed occasionally (Bliss 1982).
Despite the fact that the diversity of holding systems was demonstrated by Pérez as possibly reflecting phylogenetic relationships, only a few taxonomists have paid attention to this character in brachyuran crabs. Pearson (1908: 15, 19, fig. 3) briefly mentioned and figured the locking arrangement in *Cancer pagurus* Linné, 1758, with two small "tubercles" or "papilla" on the fifth thoracic somite. Hoestlandt (1940; 1948) studied the apparatus in *Eriocheir sinensis* H. Milne Edwards, 1854, and showed that its functionality is lost beyond a certain size of male individuals. Stauber (1945) analysed its condition in different stages of pinnotherids. Hartnoll (1965) collected information on grapsid crabs from Jamaica and described those species in which morphological structures tend to be reduced or lost. Guinot (1976: 47, 52) called attention to the press-button in the family Belliidae: in *Bellia picta* H. Milne Edwards, 1848, males are equipped with a nonfunctional apparatus.
For Hartnoll (1975), who elegantly compared the copulatory structure and function in primitive Brachyura, three different patterns of retaining systems may be recognized, exemplified by *Dromia, Homola* and *Lyreidus*. Bourne (1922: 69, pl. 4, fig. 4) was the first author to point out the system found in *Lyreidus* de Haan, 1841, that is, two "small aliform processes" on abdominal segment 6 and two small knobs on "pterygoid pro-

cesses" of sternite 5. The same feature was remarked in the genus *Lysirude* Goeke, 1986 by Feldmann & Wilson (1988: 478). The subfamily Lyreidinae was established (Guinot 1993b) by taking into account the presence of their locking mechanism, that is unique in the family Raninidae. In the Podotremata, abdominal retention by pereiopods in the dynomenid *Paradynomene tuberculata* Sakai, 1963 and the disposition in the fossil podotrematous family Dakoticancridae Rathbun, 1917 were examined (Guinot 1993a). McLay (1991; 1993) used the size and shape of uropods, and their role in the abdominal locking mechanism in dromioid crabs. Tavares (1994, 1996, 1998) was the first author to use the locking mechanism as a criterion in a cladistic analysis and described two special systems: a "sliding system" in the family Cyclodorippidae and a "stop system" in *Phyllotymolinum* Tavares, 1993, that allowed its erection as type genus of a new family, Phyllotymolinidae. Bellwood (1996: 175), who reported the presence of a press-button mechanism in the Calappidae and Hepatidae, and the absence of buttons in the Orithyiidae and Leucosiidae, also used her results in a cladistic analysis of these crabs. The present paper takes into account numerous data given by Guinot (1978a; 1979a, *cf.* table 5) who extensively investigated most of the Brachyura in respect of abdominal holding structural patterns with an evolutionary insight, and preliminary results of a thesis on the same subject that was undertaken in the Laboratoire de Zoologie, Muséum national d'Histoire naturelle (Bouchard 1996).

MODALITIES OF ABDOMINAL RETAINING AND LOCKING SYSTEMS

PODOTREMATA Guinot, 1977

Guinot (1977, 1978a, 1979a, 1991; Guinot *et al.* 1994; Guinot & Richer de Forges 1997) divided the Brachyura into three sections mainly on the basis of the location of the sexual orifices. The coxal positions of male and female gonopores, with external fertilization, were referred to as symplesiomorphies, which characterize the podotreme crabs. The presence in podotreme females of two separate reproductive ducts, one for egg laying (genital pore on P3) and one for spermatophore laying (aperture of the spermatheca at the end of the sternal suture 7/8) contrasts with the single duct in heterotreme/thoracotreme female crabs in which the sternal vulvae are the sole orifices used for egg laying, for the intromission of male pleopods (that allows internal fertilization) and for the storage of the spermatozoas. As a result of 18S rRNA analysis, Spears & Abele (1988: 2A) removed the Dromiidae from the Brachyura, arguing that the dromiids "branch very early, prior to the Anomura". Concluding that "there is no molecular support [...] for the division Podotremata (*sensu* Guinot), which groups raninids and dromiids together on the basis of a similar gonopore location", Spears, Abele & Kim (1992: 456) proposed abandoning the taxon Podotremata and placing the Raninidae at the lower limit of the Brachyura. This interpretation of the molecular data was based on the study of only four species of Podotremata, without considering any dynomenid, homolodromiid, homolid, latreilliid, cymonomid or cyclodorippid groups. But additional investigations conducted by the same authors led to another major change by considering the Dromiacea as true brachyurans to become the sister group of the Homoloidea (Spears & Abele 1996: 14bis; and oral statement in 2nd European Crustacean Conference, Liège 1996).

The question of whether the Podotremata is a monophyletic group remains topical. A parsimony analysis using mainly spermatozoal ultrastructure suggests that the Podotremata is a monophyletic taxon (Jamieson 1994). Investigations in progress (Guinot & Tavares, in preparation) support that on the one hand, Dromiacea and on the other hand, Homoloidea are basal podotremes; Raninoidea and Cyclodorippoidea *sensu* Tavares 1994 are more advanced podotremes, some of their characters resembling apomorphies of the higher Brachyura. Monophyly versus paraphyly of the Podotremata and their possible placement as the sister group of the heterotreme-thoracotreme assemblage remain open questions.

An essential apomorphy of Brachyura is the loss of the tail fan, which is present in "Macrura" and

Anomura (Lithodidae and Lomoidea excepted). In the primitive crabs, *i.e.* the Podotremata, the uropods can remain as dorsal plates (Dynomenidae and most Dromiidae) or as ventral lobes (Homolodromiidae and a few Dromiidae). Such platelike or lobelike vestiges are lost in all other families (Homolidae, Latreilliidae, Poupiniidae, Cymonomidae, Cyclodorippidae, Phyllotymolinidae, Raninidae; see Table 3, p. 683). Another robust apomorphy of the Brachyura is the abdomen, which is reduced, inverted, and folded against the ventral surface, with subsequent elimination of its locomotory function. If in certain Podotremata the abdomen is still incompletely folded, in others the pleon acquires its flexed position against the thoracic sternum. It is thus not surprising to find that in Podotremata the abdomen is retained by various devices.

Most Podotremata immobilize their abdomen by means of a tubercle, knob, elongate flange, serrated ridge, projection, or spine that arises from the thoracopod coxae (Mxp3 and/or pereiopods P1-P2 and even P3). These structures overhang the abdomen, or fit into complementary parts of the abdomen (coaptations by juxtaposition and by engagement), or act as a stop system. In all of these cases, the abdomen is prevented from slipping out. Additionally, in certain Podotremata there is a coaptation by assemblage, consisting of a fixation by abdominal sockets that fit over projections issued from thoracic sternum (sternite 4 for the homolid press-button and sternite 5 for the lyreidine projection).

Various mechanisms can simultaneously be effective in the same podotreme crab. A striking example is shown by homolids (Tables 1, 2): retention is undertaken by several structures that originate in the coxae of various appendages, probably used together, and, in addition, by a very firm press-button.

SUPERFAMILY DROMIACEA de Haan, 1833

On the basis of larval morphology, some workers had for a long time excluded the Dromiacea from the Brachyura, whereas Homoloidea and Raninoidea were retained in the Brachyura as early or pre-Brachyura (Williamson 1965, 1982; Rice 1980, 1981a, b, 1983). The same authors attempted to explain the dromiacean paradox (that is, anomuran features of the larvae and brachyuran features of the adults) by invoking horizontal gene transfer (Williamson 1988, 1992; Williamson & Rice 1996). While investigations on the copulatory structures and mating behaviour showed that the Dromiacea have evolved towards the brachyuran condition (Hartnoll 1975), the Dromiacea continued to be regarded as non-brachyuran on general morphological grounds by a few carcinologists (de Saint Laurent 1979). The controversy was increased by the first, fragmentary molecular data (Spears *et al.* 1992; see above). Scholtz & Richter (1995: 321; 1996: 14) found evidence for the monophyly of the Brachyura, including the Dromiacea, from phylogenetic analysis. The first spermatological analyses indicated that, at that stage of our investigations, if there is a distinctive dromiacean groundplan which morphologically supports the group Dromiacea, sperm structure does not clearly distinguish the constituent families Homolodromiidae, Dromiidae and Dynomenidae (Jamieson *et al.* 1995; Guinot *et al.* 1998). Consideration may have to be given to the fact that the majority of, if not all, the Dromiidae are monophyletic together with the Dynomenidae and Homolodromiidae. These spermatological results, however, need to be regarded with prudence, awaiting more extensive studies in additional taxa.

Many characters are exclusively shared by Homolodromiidae, Dromiidae and Dynomenidae, which endorse recognition of the monophyletic group Dromiacea. Dromiaceans are plesiomorphic by the persistence of a pair of appendages on each abdominal segment (in males vestigial, or sometimes lost, pleopods on pleomeres 3-5; in the two sexes, uropods on pleomere 6) in contrast to other podotremes (*i.e.* Homoloidea, Cyclodorippoidea, Raninoidea) in which pleopods and uropods in males have been lost on pleomeres 3-5 and on pleomere 6, respectively, as in the Heterotremata-Thoracotremata assemblage. It should be noted, however, that in the present paper we attempt to demonstrate the homology between the uropod and the abdominal socket, which implies that the uropod is practically never completely lost in brachyuran crabs (see Hypothesis about the homology uropod-socket, Table 3).

FAMILY HOMOLODROMIIDAE Alcock, 1900

The family, reviewed and demonstrated as monophyletic by Guinot (1995), shows a great number of plesiomorphic characters, that support the contention that it contains the most primitive members of the Podotremata.

Scholtz & Richter (1995: 322) supported the primitive status of the Homolodromiidae but went

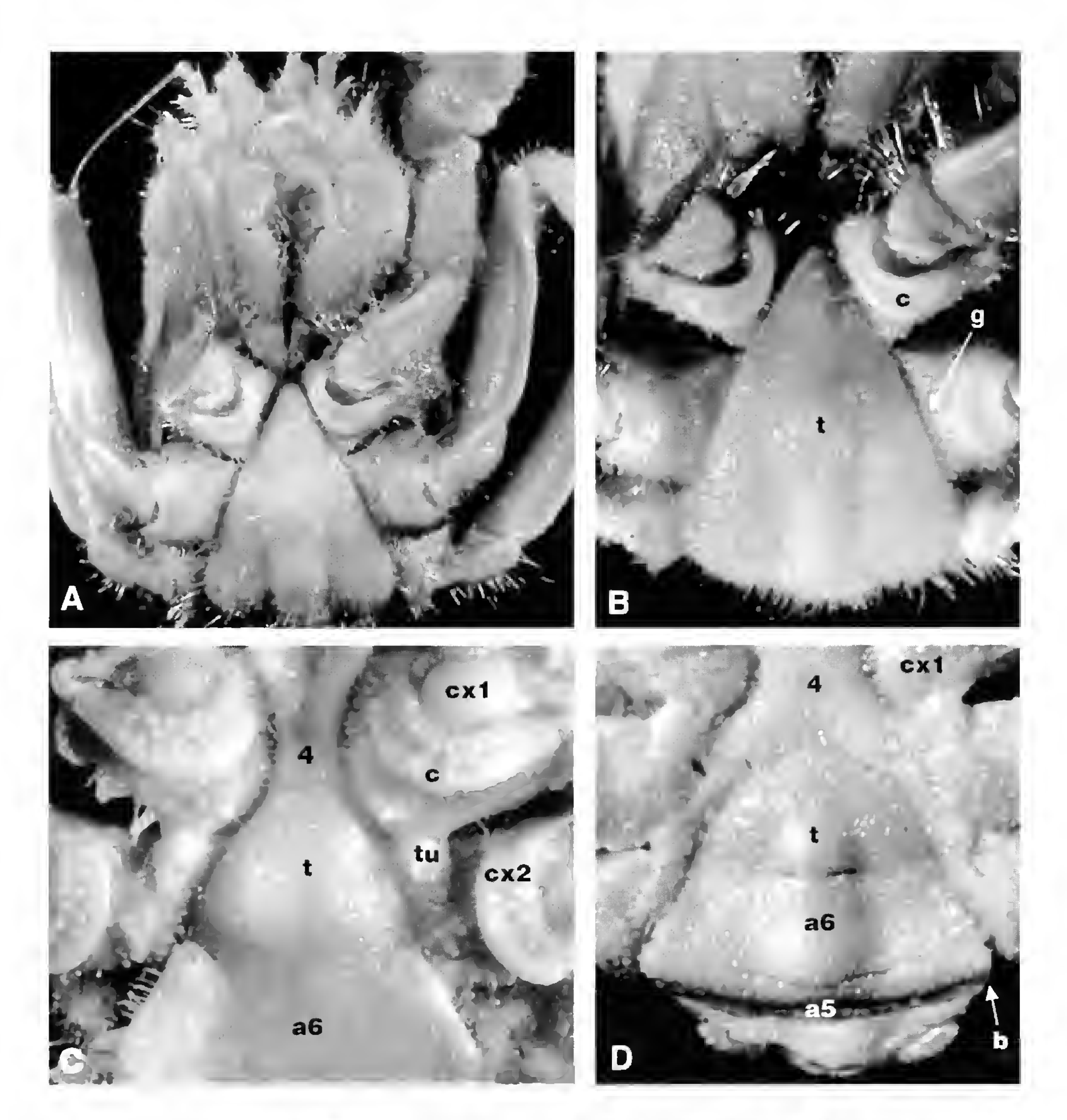


FIG. 1. — Retaining apparatus in Homolodromiidae and in *Hypoconcha* Guérin-Méneville (Dromiidae); **A**, **B**, *Dicranodromia felderi* Martin, ♀ 23 × 14 mm, in the vicinity of San Andrês, "Oregon", stn 1908 (USNM); **C**, *Hypoconcha californiensis* Bouvier, ♂ 20.3 × 19.4 mm, syntype, Gulf of California (MNHN-B 22066); **D**, *Hypoconcha arcuata* Stimpson, ♂ 12.3 × 9.3 mm, Sombrero (MNHN-B 22065). Abbreviations: **a5**, **a6**, abdominal segments 5, 6; **b**, bend at right angles of abdominal segment 5; **c**, carina; **cx1**, **cx2**, coxae of P1, P2; **g**, granules; **t**, telson; **tu**, tubercle; **4**, sternite 4.

so far as to regard homolodromiids as the sister group of all other Brachyura; however they have since returned homolodromiids to the Dromiacea (Scholtz & Richter, oral statement in the 2nd European Crustacean Conference, Liège 1996). We prefer not to separate the Homolodromiidae from the Dromiidae, even if the combination of their morphological characters is unique. The close relationship between homolodromiids, dromiids and dynomenids is complemented by the sperm characters, which show a mixture of features of these three families (Guinot *et al.* 1998).

The family Homolodromiidae consists of only two genera, *Homolodromia* A. Milne Edwards, 1880 and *Dicranodromia* A. Milne Edwards, 1880, with no more than twenty living species. But numerous homolodromiid ancestors constitute the closely related, exclusively fossil, family Prosopidae von Meyer, 1860, known from the Middle Jurassic or even earlier.

Homolodromiids are characterized by small, exclusively ventral and lobiform uropods, vestigial pleopods often present on pleomeres 3-5 in males, abdominal pleura sometimes markedly extended, and by a very long telson. The abdomen, which is inserted between the inclined walls formed by the coxae of the pereiopods, lies in a rather deep excavation between the coxae, and the pleomeres are somewhat shaped to the internal surface of the corresponding coxae. Homolodromiids have sterno-coxal depressions at the level of P2 and P3 (Guinot 1995).

In *Homolodromia paradoxa* A. Milne Edwards, 1880 the coxae of P1 and P2 are smooth and the abdomen seems simply flexed between the pereiopods. In most homolodromiids, however, there are a few granules on the coxa of P1 and some more numerous and regularly arranged granules on the coxa of P2: if they do not clearly overhang the telson, at least they perhaps restrict the sideways movements of the abdomen. In *H. kai* Guinot, 1993, *Dicranodromia karubar* Guinot, 1993 and *D. nagaii* Guinot, 1995, for example, the weakly granular coxae of P1 are clearly hollowed at their bases and the telson slides along beside them; on P2 some coxal sharp granules are located close to the abdominal margin. In *H. bouvieri* Doflein, 1904 the granules on P2 are particularly acute and come very close to the telson, being perhaps effective. In males, sometimes otherwise almost completely smooth, these granules occur only on P1 and P2 coxae. The granules are lost in mature females, in which the internal surfaces of the coxae become smooth and modified to receive the larger abdomen.

In only one species, *Dicranodromia felderi* Martin, 1990, where carinate ridges project over the ventral margins of the first pereiopods (Martin 1990, figs 1b, 1c, 3A), a unique structure has been discovered, which is similar in females and males (Guinot 1995: 250, fig. 32b) (Fig. 1A, B). The inferior part of the coxae of the chelipeds forms a distinct depression, which is surrounded by a thick, smooth, carinated and horseshoe-shaped prominence. This structure overhangs the extremity of the telson on both sides, preventing it from being lifted up, and the telson is retained by sliding through the depression. A few granules are present on the P1 coxae; more numerous and regularly arranged granules are also present on the P2 coxae.

Discussion

The carinate structure of *D. felderi* appears to be similar to that in other Podotremata in having a coxal projection from different legs that overhangs the abdomen. It is, however, developed on the whole coxa of P1 and it is smooth, not spinose. The P1 coxal keel of *D. felderi* evokes the P1 and P2 coxal carinae of *Hypoconcha californiensis* Bouvier, 1898 (Fig. 1C) (see below), the role of which remains enigmatic. If in the Homolodromiidae the differentiarion of *D. felderi* seems to be an effective retaining structure, the acute granules on the coxae of the two first pereiopods, specially on P2, could be also interpreted as structures involved in retaining the abdomen (Bouchard 1996).

It will be valuable to look at the numerous fossil prosopid forms to verify whether such structures are present.

FAMILY DROMIIDAE de Haan, 1833

The extensive revision of the sponge crabs by McLay (1993) did not support their exclusion from the Brachyura and their association with the Anomura. Evoking the complex evolutionary relationships among more than hundred Atlantic,

Indian and Pacific species distributed in about thirty genera, McLay (1993) did not subscribe to the paraphyly of the family. Only the placement of the genus *Hypoconcha* Guérin-Méneville, 1854, was considered doubtful. The question is to know if *Hypoconcha* is related or not to another dromiid, *Conchoecetes* Stimpson, 1858, which shares with the *Hypoconcha* species an unusual camouflage habit of carrying a bivalve shell. Analysis of the problem suggests that *Hypconcha* probably belongs in the Dromiidae (McLay 1993: 229).

We will follow here the new generic arrangement proposed by McLay (1993) where attention was paid to "the size and shape of uropods in relation to their role in the abdominal locking mechanism". In dromiids the still articulated, sometimes mobile, uropods are (more or less) functional only when they consist of dorsal plates, which is the case in most genera/species. Very few dromiid species are devoid of any apparent retaining structures.

If a true sterno-abdominal cavity is lacking in dromiids, the abdomen often settles itself by its posterior part in the deep depression formed by the inclined sides of the coxae of P1-P2. The uropods are markedly sexually dimorphic in shape and size. In males and in young females uropods are more or less laterally prominent and visible dorsally, whereas in mature females they usually seem transversally extended, intercalated between the segment 6 and the telson, and somewhat concealed in the general outline of the enlarged abdomen. The telson also is sexually dimorphic, being longer and narrower in adult males.

Dromiids display several means of abdomen retention, that involve the differentiation of one or several parts of the pereiopods and abdomen. In addition to the variable structures projecting from the coxae of the two first pereiopods, the vestigial uropods may be involved. The significant role of the uropods in dromiid males is correlated with their sideways projection beyond the lateral margins of the abdomen.

Some examples of the dromiid devices are here described.

Structures on P1 only

The case of the abdomen being retained only by one pair of legs, in this case P1, is found in species of the shell-carrying genus *Hypoconcha* Guérin-Méneville, in which the broad and angular abdomen has distinct pleura and where the uropods are reduced to two very minute plates intercalated ventrally, not visible dorsally.

In *H. californiensis* (Fig. 1C) the coxa of P1 bears a group of spinous tubercles, the strongest of which overhangs the external border of the telson in its half posterior part and holds it. The role of the curious keels on the coxae of P1 and P2 found in *H. californiensis* is enigmatic and evokes the case of *Dicranodromia felderi* (Fig. 1A, B); such marked carinate structures are not present in all *Hypoconcha* species. In the genus *Hypo-concha, H. arcuata* Stimpson, 1858 (Fig. 1D) and *H. panamensis* Smith, 1869 have no coxal projections, and their system of abdominal retention is special. The male abdomen is short, with the tip of the telson reaching the level of P2, and the posterior part of segment 5, close to the articulation with segment 6, is bent at right angles so that the posterior part of the abdomen (posterior part of segment 5, segment 6, and telson) lies flat on the ventral surface.

In the dromiid *Haledromia bicavernosa* (Zietz, 1887) (species not examined), with a special combination of characters (in particular widened carapace, small and concealed uropods, and, probably, direct development), McLay (1993: 158, table 2) described a retaining apparatus that involves a blunt "tooth on bases of first legs against margin of penultimate [abdominal] segment."

Structures on P1 and P2

Both structures functional.

In *Lauridromia dehaani* (Rathbun, 1923) (Fig. 2A, B) the coxae of P1 and P2 each have a denticulated prominence which fits into a depression on the external margin of the telson and the somite 6, respectively. In a ventral view of the abdomen, along the external margin and just posterior to the uropod, a notch on the telson receives a coxal prominence of P1 while a deep depression receives a coxal prominence of P2. In addition, the mobile uropod is involved, being engaged against the bases of the coxa of P2. When the abdomen is extended, the pair of coxal

prominences on P2 acts as in full-lock with the pair of uropods. Thus, here, the uropod plays an important role.

It is not clear why specimens of *L. dehaani* examined by Dai & Ng (1997: 757) are indicated as having a serrated flange "obvious only on the coxa of the first leg."

Structures on P1 supposed nonfunctional

In *Lauridromia intermedia* (Laurie, 1906) (Fig. 2C) the abdomen settles tightly between the bases of the first pereiopods, the coxa of which bears a granular prominence, probably not functional; on the external margin of the telson the corresponding area is not notched. In compensation, the well-developed coxal prominence of P2, which bears a fine and regularly denticulated crest, fits into a deeply excavated depression on the lateral edge of abdominal segment 6. The narrow uropod finds its place perfectly in contact with the coxal projection, and the abdomen is firmly retained at this level. The internal side of the P3 coxa bears a nonfunctional minute granule. Additionally, on the sternum two areas are differentiated, one with sparse granules at the level of the P1 condylus and another one with a tuberculate crest at the level of the P2 condylus.

Variations exist concerning the relative position of the uropod in regard to the coxal projection of P2. In *Takedromia cristatipes* (T. Sakai, 1969) the high coxal prominence on P2 comes into contact with the uropod, which is movable.

In *Dromia erythropus* (G. Edwards, 1771) (Fig. 2D) and in *D. marmorea* Forest, 1974, the uropod lies rather far from the coxal prominence. A similar organization is observed in *D. monodi* Forest *et* Guinot, 1966 (Fig. 3A), which has specially mobile uropods and a coxal prominence on P2 bearing 8-10 small denticles aligned on a high oblique crest. The coxa of P1 remains tuberculate but does not seem to be effective since there is no contact with the telson. In *D. monodi* some granules are also present on the lateral part of the sternite 4. In his diagnosis of the genus *Dromia* Weber, 1795, McLay (1993: 149) mentioned the uropods as "used in male abdominal locking mechanism by fitting in front of serrated flange on the bases of first legs", a sentence that led Dai & Ng (1997: 757) to misinterpret "this serrated flange supposedly present only on the coxa of the first leg."

Homalodromia coppingeri Miers, 1884 (Fig. 3B) has longitudinally extended and pointed uropods, that are clearly mobile. On the P1 coxa there is a small tuberculate prominence and on the P2 coxa a particularly high, cupuliform, and denticulated prominence that is nearly horizontal at rest and becomes functional by the movement of the leg. This prominence constitutes a full-lock system with uropods; the long telson is not involved.

The structure on the P1 coxae of *Dromia personata* (Linné, 1758) (Fig. 4B) and *D. bollorei* Forest, 1974, which consists of a small granular prominence far from the abdomen's margin, is not functional. The salient granular prominence on the P2 coxa comes in contact with the border of segment 6 and is distant from the mobile uropod. The abdomen of the preserved specimens examined was not retained.

Only the observation of living animals may help to conclude how efficient the mobile uropods are as a full-lock mechanism.

Structures on P2 and P3

When the abdomen is short and the telson's tip lies far from the level of the chelipeds, nothing functional is observed on the P1 coxa, and structures on P2 and P3 are present instead.

In *Conchoecetes intermedius* Lewinsohn, 1984 (Fig. 4A), a bivalve-carrying crab, the P2 coxa bears a strong and ornamented prominence that acts as a full-lock mechanism with a very close, salient uropod. The narrow episternite 5, which remains exposed and visible between the coxae of P2 and P3, is also provided with some granules. In addition, a rounded tubercle (the internal one of an aligned series) on the P3 coxa comes into contact with an incurved part of the lateral abdominal margin at the level of segment 5. Similar granules on the P4 coxae (the legs that hold the shell) are too small to be effective.

In *Sphaerodromia* Alcock, 1899, which is considered the most primitive known dromiid genus by McLay (1993: 127), individuals carry large pieces of sponge for camouflage. McLay (1991: 466) reported a relatively "elaborate grasping mechanism" in the genus. All preserved speci-

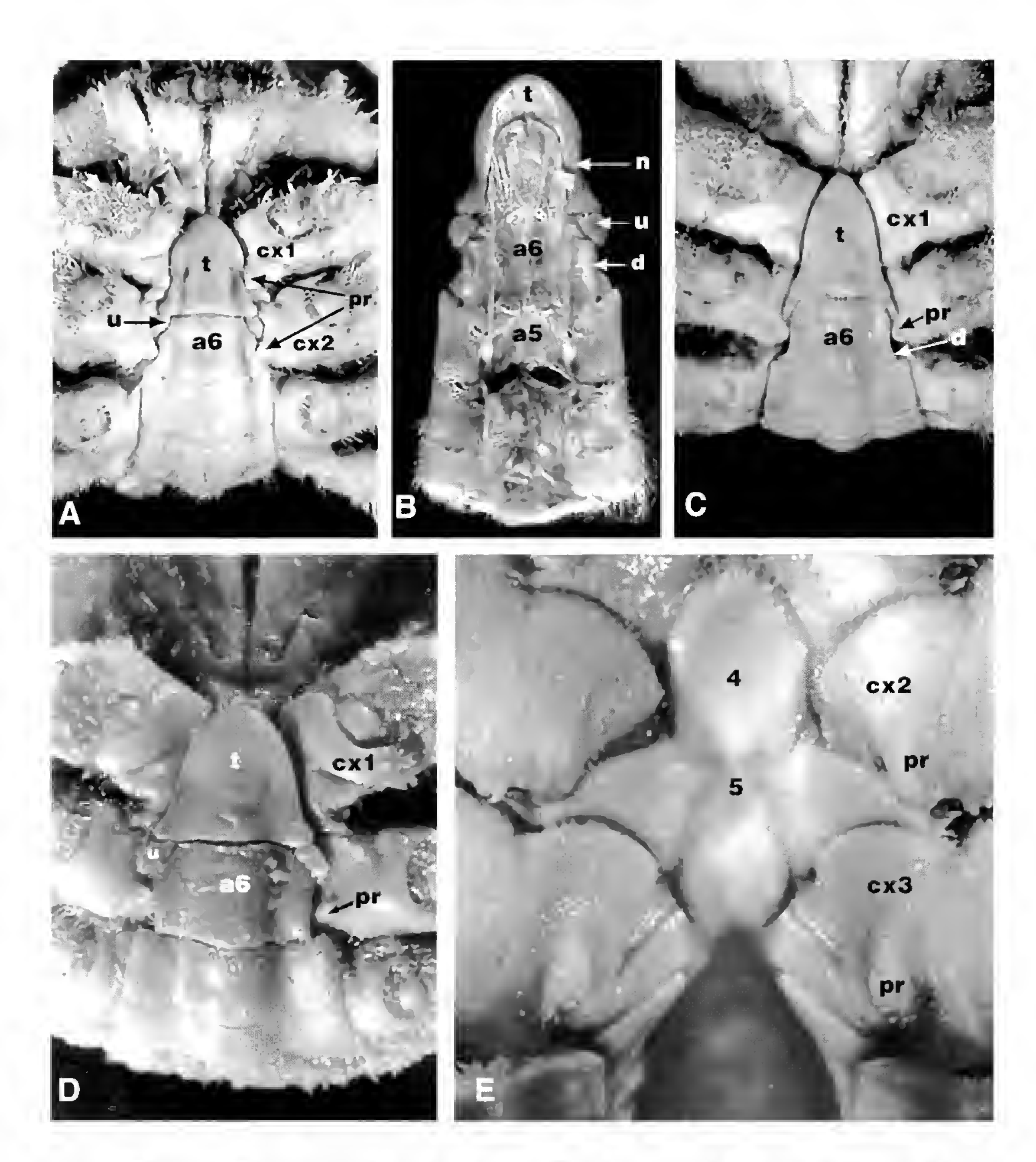


FIG. 2. — Retaining apparatus in Dromiidae: **A**, **B**, *Lauridromia dehaani* (Rathbun); **A**, ♂ 80.4 × 76.9 mm, Seychelles (MNHN-B 7760); **B**, ♂ 42 × 45 mm, Gulf of Suez (MNHN-B 21994): internal surface of abdomen; **C**, *Lauridromia intermedia* (Laurie), ♂ 52.4 × 48.1 mm, New Caledonia (MNHN-B 12754); **D**, *Dromia erythropus* (G. Edwards), ♂ 25.2 × 25.3 mm, Venezuela (MNHN-B 12713); **E**, *Sphaerodromia nux* Alcock, ♂ 58.7 × 67.1 mm, Madagascar (MNHN-B 6872): without abdomen. Abbreviations: **a5**, **a6**, abdominal segments 5-6; **cx1**, **cx2**, **cx3**, coxae of P1-P3; **d**, depression; **n**, notch; **pr**, projection of the coxa, **t**, telson; **u**, uropod; **4**, **5**, sternites 4, 5.

mens that were examined did not have their abdomens well retained. We did not observe any specialized structures on the P1 coxa of *S. nux* Alcock, 1899 (Fig. 2E), *S. ducoussoi* McLay, 1991 and *S. brizops* McLay *et* Crosnier, 1991. On the coxae of P2 there is a distinctly granular prominence that acts on anterior part of the telson (the dorsal uropods are not involved); on the coxa of P3 there is a larger granular prominence, that is, however, completely covered by abdominal segment 5.

Structures on P2 only

In *Hemisphaerodromia monodus* (Stebbing, 1918) (Fig. 3C, D), which has a narrowed abdominal segment 6 and mobile dorsal uropods, the whole base of the P2 coxa forms a rounded and salient prominence, that is serrated on its internal and superior margins. This prominence is tigthly encircled in the space just behind the uropods and fits into a depression on the border of pleomere 6, much thickened at this level.

In *Cryptodromiopsis antillensis* (Stimpson, 1858) (Fig. 4C), in which the dorsal uropods apparently do not play a role, a short but sufficiently developed spine that projects from the base of the P2 coxa overhangs segment 6 anteriorly and firmly holds the abdomen. It is noteworthy that a markedly visible granule is present on the P3 and P4 coxae.

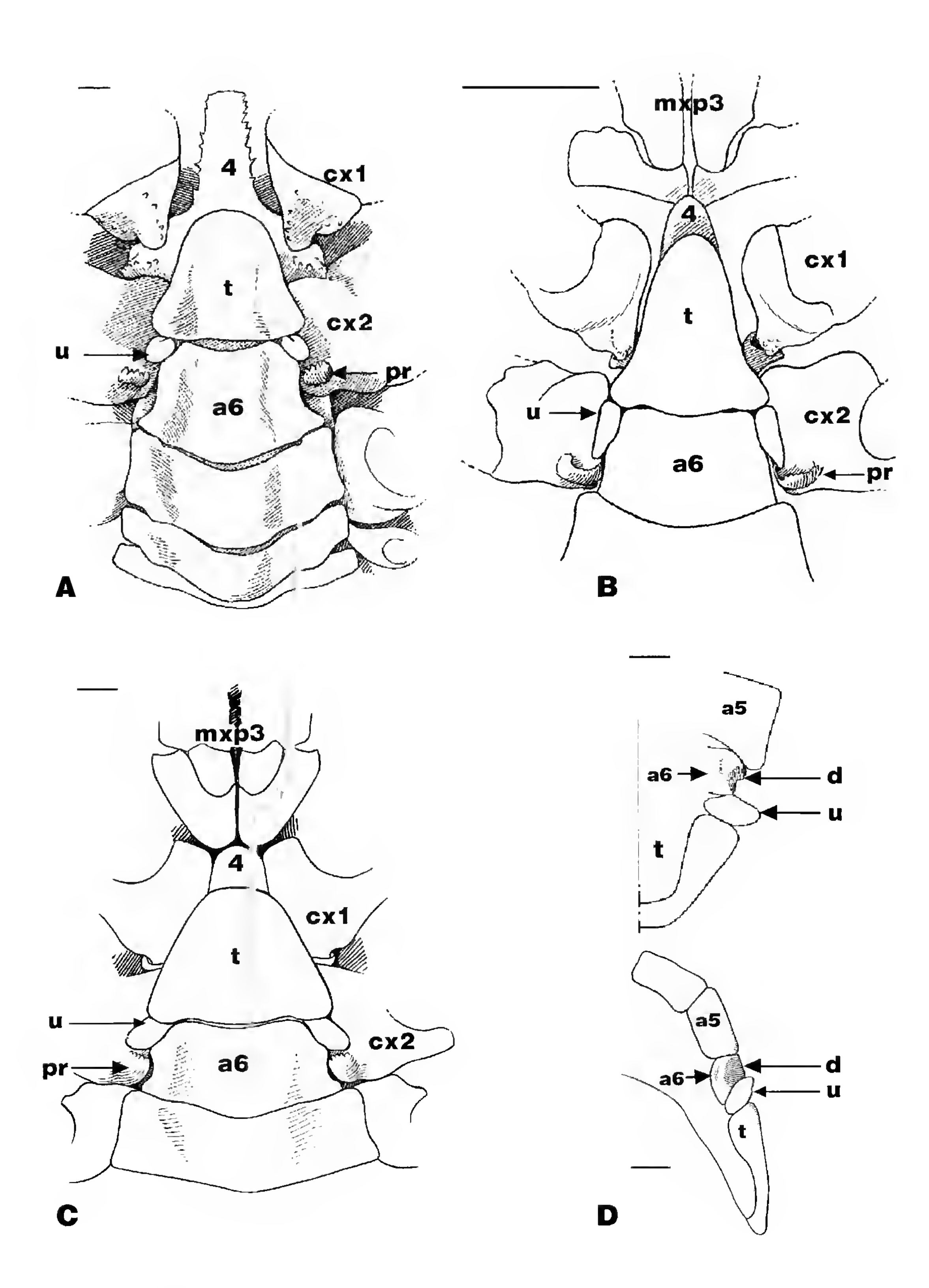
The three known species of *Exodromidia* Stebbing, 1905, *E. spinosa* (Studer, 1883), the type species of the genus, *E. bicornis* (Studer, 1883) and *E. spinosissima* (Kensley, 1977), all from South Africa, were examined. They are characterized by vestigial male pleopods on segments 3-5 (not discernible, however, in our small-sized male of *E. spinosa*) and by uropods that are only small ventral lobes and cannot play any role in retaining the abdomen. All three show a highly marked differentiation of the coxae of P2 (Guinot 1995: 187), a feature that was neglected in the taxonomic descriptions. In *E. bicornis* (Figs 4D, 5A), a very long, stout, smooth (and white) spine projects from the coxa of P2 in a direction parallel to the lateral margin of the abdomen. In *E. spinosissima* (Fig. 5B, C) the P2 projection is relatively thicker and tuberculate at its base, and similarly directed. This projection overhangs abdominal segment 5 and the posterior portion of segment 4 only when the P2 are moved backwards. The presence of such strong coxal projections is unique in dromiids. Their role in preventing the abdomen being lifted up is evident, and significantly implies an active involvement of the legs (*i.e.* P2) in order to place the long spines above the abdomen.

Exodromidia spinosa (Studer, 1883) (Fig. 5D, E) shows a rounded and granular prominence that projects from the P2 coxa and fits into a deep depression on the margin of abdominal segment 6. This segment is distinctly hollowed along most of its thickened edge. The coxal projection is visible on the illustration given by Doflein (1904, pl. 6, fig. 2); the depression on pleomere 6 and the telson's spine are not visible in the sketches by Macpherson (1983: 13, fig. 6A). The modification of the external edge of pleomere 6 resembles that of *Hemisphaerodromia* (Fig. 3C, D), but a difference lies in the fact that mobile dorsal uropods are involved in *Hemisphaerodromia*, whereas absolutely not in *E. spinosa* (only small ventral lobes).

The three *Exodromidia* species have the posterior part of telson ending in an acutely sharp spine in males (Figs 4D, 5A, B, D) but rounded in females. The acute tip moves inside a marked furrow that is hollowed on sternite 4 in males, whereas sternite 4 is not grooved in females. The furrow of sternite 4 could be particularly "useful" when in *E. bicornis* and *E. spinosissima* the pair of long coxal projections must overhang the abdomen at times when free movement of the abdomen is necessary.

E. bicornis, chelipeds of which are considerably elongated, evidence of strong positive allometric growth, is a peculiar dromiid: bits of coral are attached to the long pseudorostral teeth, and the whole body is concealed by fragments of sand or

FIG. 3. — Retaining apparatus in Dromiidae. **A**. *Dromia monodi* Forest *et* Guinot, ♂ 30 × 32 mm, Mission Casamance (MNHN-B 21937); **B**. *Homalodromia coppingeri* Miers, ♂ 5.2 × 5.3 mm, Seychelles (MNHN-B 26130); **C, D**. *Hemisphaerodromia monodus* (Stebbing), ♂ 14 × 15.5 mm, Fort-Dauphin (MNHN-B 11204); in **D** detail of abdomen, ventral (above) and side (below) views. Abbreviations. **a5**, **a6**, abdominal segments 5, 6; **cx1**, **cx2**, coxae of P1, P2; **d**, depression; **mxp3**, external maxilliped; **pr**, projection; **t**, telson; **u**, uropod; **4**, sternite 4. Setae were not figured. Scale bars: 1mm.


4
cx1
t
cx2
u
pr
a6
A
mxp3
4
cx1
t
u
cx2
a6
pr
B
mxp3
4
cx1
t
u
cx2
pr
a6
C
a5
a6
d
u
t
a5
d
a6
u
t
D

mud among the stiff bristles and spines. Carrying behaviour with the very short, but subcheliform, last pereiopods is possible, but perhaps unnecessary (Guinot *et al.* 1995). *E. spinosa* also has long chelipeds and the carapace covered with stiff bristles, but materials of settlement were not observed on the body of the two specimens that were examined.

No apparent structures

In the species of *Pseudodromia* Stimpson, 1858 that were examined, *P. latens* Stimpson, 1858 and *P. rotunda* (Macleay, 1838), which are always intimately associated with ascidians, and in the monospecific genus *Ascidiophilus* Richters, 1880 (with *A. caphyraeformis* Richters, 1880, a small-sized species with the body tightly enclosed in a

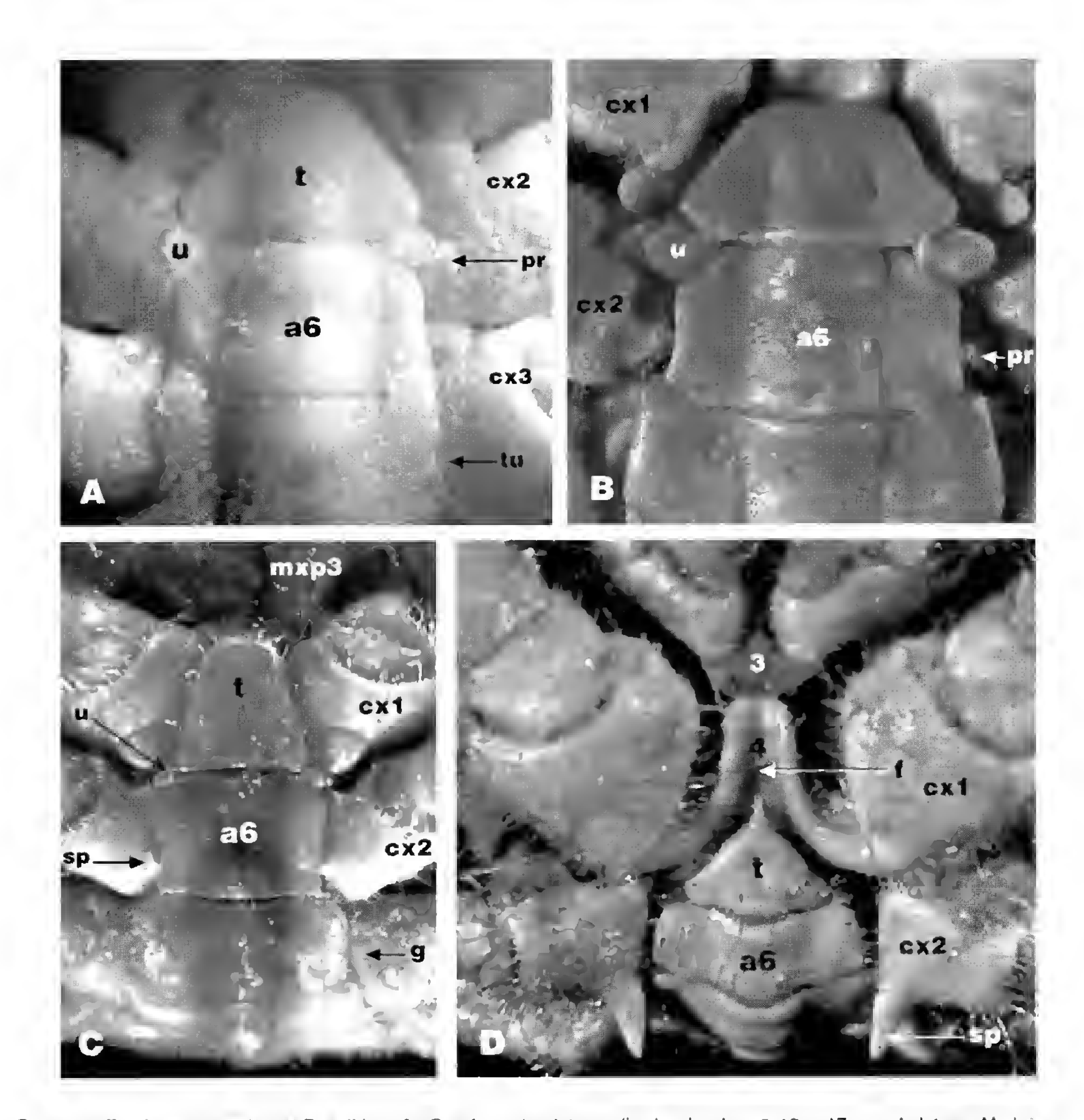


Fig. 4. — Retaining apparatus in Dromiidae; **A**, *Conchoecetes intermedius* Lewinsohn, ♂ 16 × 17 mm, holotype, Madagascar (MNHN-B 6891); **B**, *Dromia personata* (Linné), ♂ 52 × 65 mm, Azores, Faial (MNHN-B 21969); **C**, *Cryptodromiopsis antillensis* (Stimpson), ♂ 18 × 18 mm, French Guyana (MNHN-B 22029); **D**, *Exodromidia bicornis* (Studer), ♂ 18 (without pseudorostral spines) × 19 mm, Souh Africa (SAM 10724). Abbreviations: **a6**, abdominal segment 6; **cx1**, **cx2**, **cx3**, coxae of P1-P3; **f**, furrow on sternite 4; **g**, granule; **mxp3**, external maxillipeo; **pr**, prominence; **sp**, spine; **t**, telson; **tu**, tubercle; **u**, uropod; **3**, **4**, sternites 3, 4.

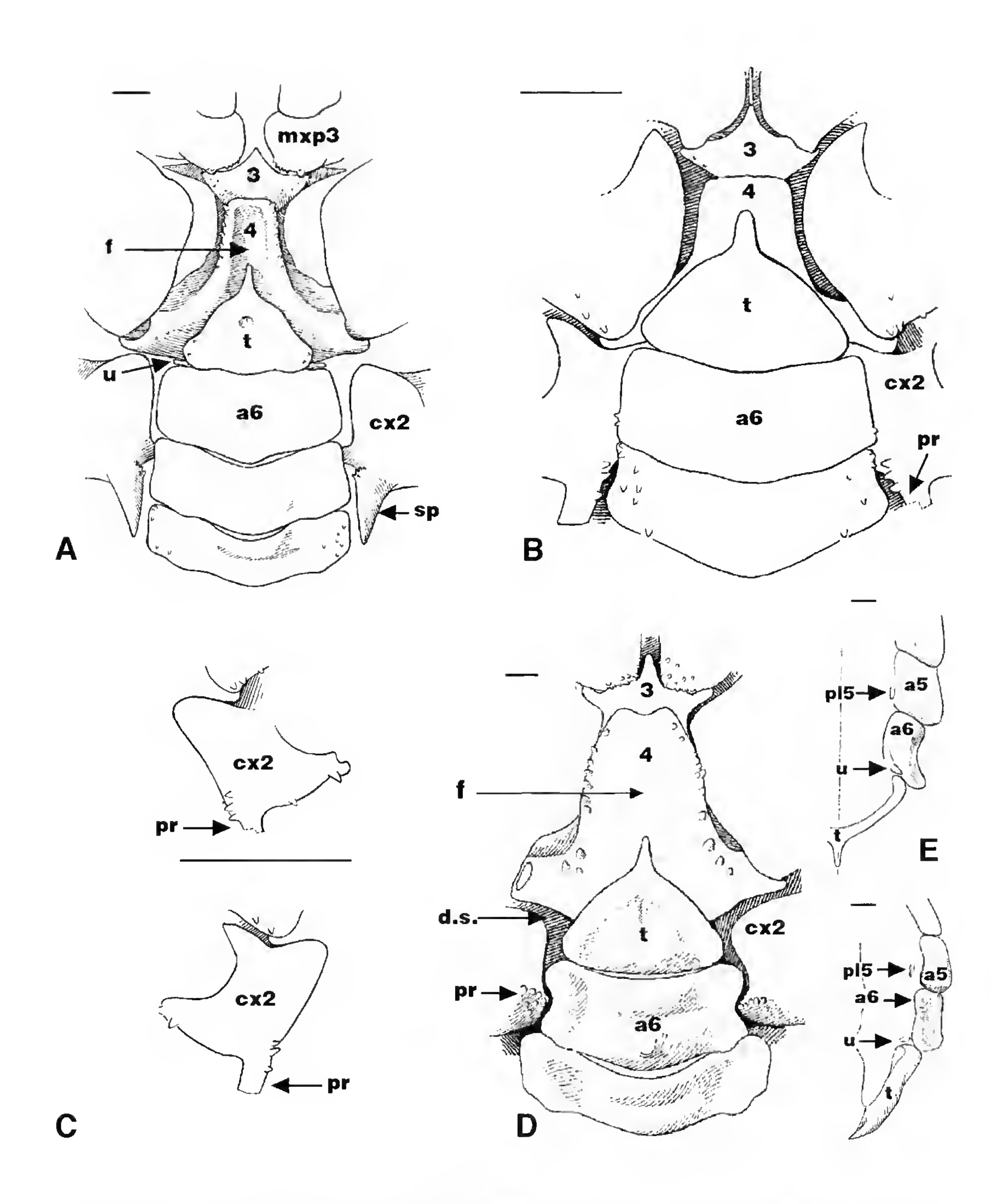


FIG. 5. — Retaining apparatus in the three species of *Exodromidia* Stebbing (Dromiidae). **A**, *Exodromidia bicornis* (Studer), ♂ 18 (without pseudorostral spines) × 19 mm, South Africa (SAM A10724); **B**, **C**, *Exodromidia spinosissima* (Kensley), ♂ 4.8 × 4.6 mm, South Africa (SAM A17681); in **C**, detail of right and left P2 coxae (the projections are broken at their tips, at least on coxa of left P2); **D**, **E**, *Exodromidia spinosa* (Studer), ♂ 29 × 32 mm, Cape Point (BMNH 1929.12.1.234-235); in **E**, detail of abdomen in ventral (above) and side (below) views. Abbreviations: **a5**, **a6**, abdominal segments 5, 6; **cx2**, coxae of P2; **d.s.**, sterno-coxal depression; **f**, furrow; **mxp3**, external maxilliped; **pl5**, vestigial pleopod on abdominal segment 5; **pr**, projection, **sp**, spine; **t**, telson; **u**, uropod; **3**, **4**, sternites 3, 4. Setae were not figured. Scale bars: A, C, D, 1 mm; B, 0.5 mm; E, 2 mm.

compound ascidian held by the prehensile P4 and P5, see Guinot 1995), the absence of an abdominal retention in males can be inferred by the protection obtained by living inside the ascidian. In these highly specialized forms, the vestigial pleopods on segments 3-5 are lost. The uropods are only represented by small ventral lobes in *Pseudodromia*, whereas there is no trace of uropods in *Ascidiophilus*.

Tunedromia yamashitai (Takeda *et* Miyake, 1970), type species of the genus *Tunedromia* McLay, 1993, and only known from females, is indicated as lacking uropods (McLay 1993: 134, table 1), but males need to be examinated.

Discussion

The case in which only P1 is involved, retention of the abdomen at the level of the telson characterizes *Hypoconcha californiensis*. In other cases, the involvement of other appendages (P2 and/or P3) and of the dorsal uropods frees the P1 from a retaining function. In *Exodromidia*, which lacks dorsal uropods, only P2 is involved. Only when the coxal structure on P1 plays a role, an involvement of the telson was observed with a subsequent modification of its edge, which can be markedly thickened, notched or hollowed (coaptation by juxtaposition or by engagement). In the dromiid evolutionary series, the loss of the retaining function of the abdomen by the chelipeds seems correlated with the loss of the holding at the level of the telson. Thus the only appendages able to play this role, by means of a coxal projection, are P2 and P3. The P4, which in dromiids are reduced and along with P5 hold a camouflage cap, cannot be used for abdominal retention. The P2, which develop the most complex and probably the most efficient systems, remain the only appendages to be used. At this stage, the sternal somite involved in retaining is the fifth (corresponding to P2) and the involved pleomere is the sixth. In the case where the coxal prominences on P2 and P3 (*Sphaerodromia*) are completely covered by the abdomen, these structures are similar to those in the preceding cases although they are ineffective.

As in all Brachyura the abdomen is used for the protection of the eggs in female dromiids. In the family Dromiidae the sexual dimorphism of uropods concerns not only the size (uropods are generally smaller in males) but also the shape and orientation (uropods are generally more salient in males), so that the role of the uropods remains very efficient in adult males.

Among the numerous modalities of abdominal retention shown by dromiids, we observed cases in which the abdomen, simply applied flat on the sternum between the legs, is more or less efficiently immobilized by a prominence that acts as a stop, often with horizontally expanded uropods (*Conchoecetes*, *Dromia personata*, *D. bollorei*, *D. monodi*). In other cases (*Lauridromia*), the abdomen, with almost vertical uropods, is inserted in a rather deep depression between the legs, and the edges of the telson and segment 6 become highly modified complementary to the corresponding coxae. Coaptations by juxtaposition and by engagement perform an extremely efficient way of retaining the abdomen. We suggest to name the configuration in which the uropods contact with coxal prominences, as the full-lock system.

The case of *Hemisphaerodromia monodus* combines a coaptation by engagement (the thick border of pleomere 6 is distinctly hollowed) and a full-lock between the serrated prominences and the very mobile dorsal uropods. This configuration provides a strong system.

The uropods are very mobile in many cases (for example *Dromia personata*, *D. bollorei*, *D. monodi*, *Lauridromia dehaani*, *Homalodromia coppingeri*, *Hemisphaerodromia monodus*), and this is probably correlated with their role in abdominal retention.

Other modalities are exemplified by cases of simple overhanging, without any coaptation between the abdomen and the coxae of legs, and without the involvement of uropods (*Cryptodromiopsis antillensis*, *Exodromidia*). The coxal P2 projection in *E. bicornis* and *E. spinosissima* appears as the most developed amongst the dromiids and perhaps in all brachyuran crabs.

The abdominal segment 6 may be markedly modified in relation to its involvement in retaining the abdomen. Its thickened external edge is distinctly hollowed in *Lauridromia dehaani*, *L. intermedia*, *Hemisphaerodromia monodus* and *Exodromidia spinosa*.

Modifications of the telson in relation to the retaining apparatus are sometimes pronounced in dromiids: an example is the deep notch on the external margin in *Lauridromia dehaani*. In the genus *Exodromidia*, it seems that the sexually dimorphic telson may play a role when it moves inside the furrow on sternite 4 to put the P2 coxae in an overhanging position. This depression of sternite 4, absent in females, also constitutes a sexually dimorphic feature and, if it is really involved in facilitating the accommodation of the telson spine, it is also an exceptional phenomenon in brachyuran crabs.
The cases with no apparent retaining structures in dromiids are rare. As far as we know, it only exists in species associated with ascidians, viz. *Pseudodromia rotunda* and *Ascidiophilus caphyraeformis*. *Hypoconcha arcuata* and *H. panamensis* also lack differentiated structures, but they markedly differ in having their abdomen bent at right angles, and with its posterior half particularly oriented to the ventral surface. This abdominal curvature, less pronounced in males than in females, seems to be correlated with the inclination of the two last thoracic sternites relative to the preceding ones.

FAMILY DYNOMENIDAE Ortmann, 1892
The phylogenetic relationships of the family Dynomenidae to both Homolodromiidae and Dromiidae (exemplified by *Dynomene tanensis* Yokoya, 1933, *Homolodromia kai* Guinot, 1993, and *Sphaerodromia lamellata* Crosnier, 1994, respectively), have been examined using spermatological characters (Guinot *et al.* 1998). As in the case of general morphology the ultrastructure of spermatozoa strongly endorses monophyly of the Dromiacea, without a clear recognition of its three families, however.
The question of the existence of a retaining apparatus in dynomenids was first raised by Guinot (1978a, 1979a, 1993a); see also McLay (1991).
In dynomenids the thoracic sternum is relatively wider than in dromiids and forms a plate that inclines posteriorly. The only sternite that is placed in a plane other than the preceding ones is the sternite 8, which corresponds to the last pair of legs. The P5, which are reduced but are neither dorsal nor specially movable (but their movements are coordinated with those of the other pereiopods, C. L. McLay pers. comm.), are always intercalated between the posterolateral margins of the carapace and the bases of P4. A sterno-abdominal cavity *sensu stricto* is not present. The abdomen is very broad, even in males, relatively much broader than in dromiids, flexible, and is not closely held on the sternum. The dynomenid abdomen is the most primitive one within the Brachyura in maintaining pleopods on segments 3-5 as (generally) biramous vestiges. Dorsal uropods are always well-developed, never projected, even in males, and they show sexual dimorphism, being larger in females. In preserved dynomenids, at least in adult individuals, the male abdomen is never firmly held against the sternum, resembling the female condition.

Apparatus on the coxae of thoracopods
An example of an effective retaining apparatus is shown by *Acanthodromia erinacea* A. Milne Edwards, 1880, a species ornamented with many spines. In the single mature female examined, the broad and curved abdomen covers the whole sternum, and the developed telson covers the proximal part of Mxp3 (Figs 6A, 7A, B). The coxae of four thoracopods are involved. The coxa of Mxp3 bears a particular spinule, stronger than the surrounding ones, which overhangs the posterior part of the long telson. The coxae of the three first pereiopods (P1-P3) present a lateral depression that props up the abdomen. In addition, each coxa is equipped with two to three ornaments (spinules or granules) that overhang the telson at P1-P2 level and the pleomere 6 with its uropods at the P3 level. On episternite 5, which is covered by the telson, two small granules are present but they seem not to play any role. This configuration in females is probably similar to that found in males, which were not examined.
In other dynomenids, in which the abdomen is much shorter and tends to not entirely cover the sternal plate, some structures were observed which can be referred to as a retaining system, that is perhaps inefficient at least in large adults. According to species, it involves either P2 + P3 (never P1) or sternite 5, and two main types may be described: one analogous to *Acanthodromia* and another one (see below, Apparatus on the sternum).

In two *Dynomene* species, two weak and ornamented coxal prominences occur on P2 and P3, respectively, in the adult males. In *D. tanensis* Yokoya, 1933 (Figs 6B, 7C) there is a well-developed and tuberculate prominence located on the P2 coxa that comes very close to the uropod margin; another coxal prominence exists on P3, but it is even smaller. In a male individual from Glorieuses Islands identified as *Dynomene* aff. *devaneyi* Takeda, 1977 (Fig. 6C), the coxae of P2 and P3 bear a weak prominence, the ornamentation of which is asymmetrical: on the left P2

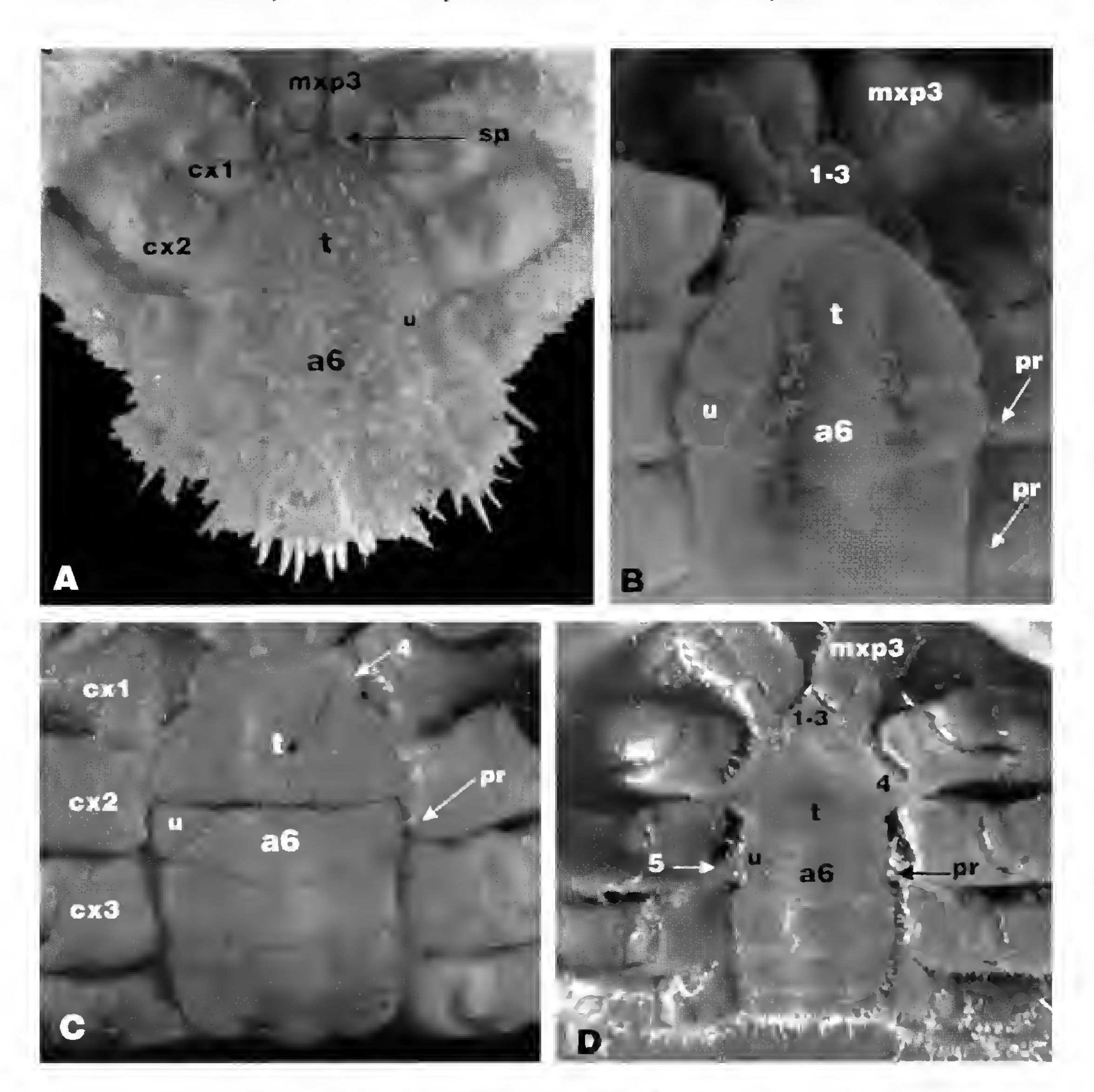


Fig. 6. — Retaining apparatus in Dynomenidae: **A**, *Acanthodromia erinacea* A. Milne Edwards, ovigerous ♀ 14.7 × 12 mm, west of Puerto Rico (USNM 124263); **B**, *Dynomene tanensis* Yokoya, ♂ 19.4 × 19.7 mm, New Caledonia (MNHN-B 25583); **C**, *Dynomene* aff. *devaneyi* Takeda, ♂ 23.2 × 22.7 mm, Glorieuses Islands, Benthedi Exp. 1977 (MNHN-B 22510); **D**, *Dynomene hispida* Guérin-Méneville, ♂ 8.8 × 11.5 mm, New Caledonia (MNHN-B 22091). Abbreviations: **a6**, abdominal segment 6; **cx1**, **cx2**, **cx3**, coxae of P1-P3; **mxp3**, external maxilliped; **pr**, coxal or sternal prominence; **sp**, spine; **t**, telson; **u**, uropod; **1-3**, sternites 1-3; **4**, **5**, sternites 4, 5.

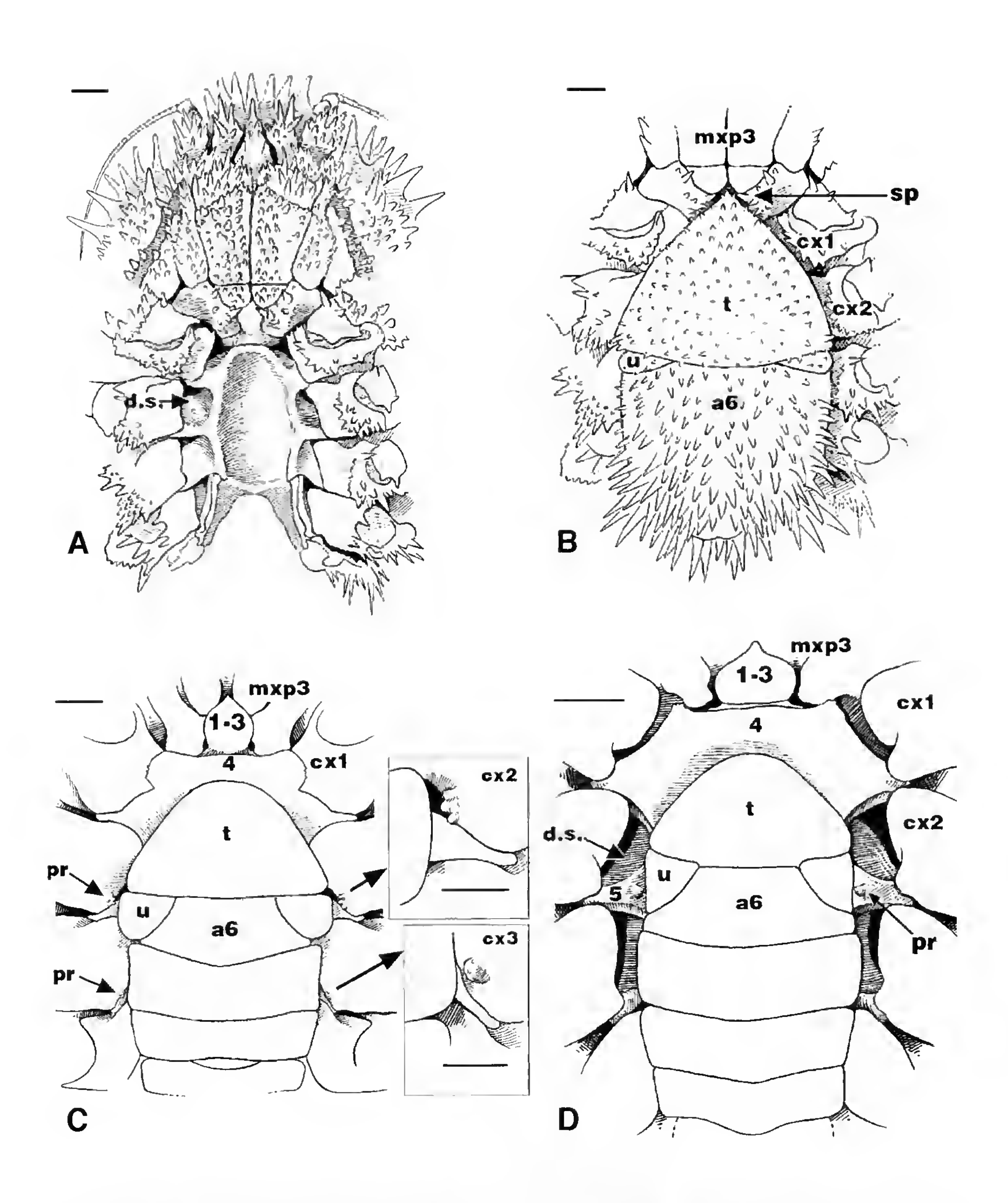


FIG. 7. — Retaining apparatus in Dynomenidae: **A**, **B**, *Acanthodromia erinacea* A. Milne Edwards, ovigerous ♀ 14.7 × 12 mm, west of Puerto Rico (USNM 124263): thoracic sternum with and without abdomen; **C**, *Dynomene tanensis* Yokoya, ♂ 12.2 × 13 mm, New Caledonia, Smib 2, stn DW1 (MNHN), with detail of the prominences on P2 and P3 coxae; **D**, *Dynomene hispida* Guérin-Méneville, ♂ 6.9 × 8.8 mm, New Caledonia (MNHN-B 22091). Abbreviations: **a6**, abdominal segment 6; **cx1**, **cx2**, **cx3**, coxae of P1-P3; **d.s.**, sterno-coxal depression; **mxp3**, external maxilliped; **pr**, projection; **sp**, spinule; **t**, telson, **u**, uropod; **1-3**, sternites 1-3; **4**, **5**, sternites 4, 5. Setae were not figured. Scale bars: 1 mm.

coxa, the prominence is distinctly bifid; on the right P2 coxa and on the left P3 coxa, the prominence has only one tubercle, and on the right P3 coxa the prominence shows a row of three tubercles. The complete system appears not to be effective. The presence of "blunt teeth" on the P2 and P3 coxae was noticed by McLay (1991: 466) in *D. devaneyi* Takeda, 1977.

The case of *Paradynomene tuberculata* T. Sakai, 1963 (Guinot 1993a), the body of which is completely covered by large granules, is difficult to analyse. The external margin of the abdomen comes close to P2 and P3 coxae, and only the very external part of the episternite 5 is visible when the abdomen is flexed. The sets of granules at the prominent bases of the P2 and P3 coxae appear as possible means of restricting the lateral movements of the abdomen. The episternite 5 is ornamented with a few sparse granules which do not appear to be effective.

Apparatus on the sternum

In male *Dynomene hispida* Guérin-Méneville, 1832, type species of the genus *Dynomene*, the differentiation is located on the narrow exposed episternite 5 (Figs 6D, 7D). Sometimes its surface seems to be granular or formed by more than one tubercle or spine. This prominence on sternite 5 lies close to the uropod; it is possible that in the juveniles it overhangs the uropod. But the prominence becomes more minute in larger individuals, and it seems to be in relation to the uropod (Guinot 1979a, pl. 21, figs 8, 9).

The same configuration of a sternal tubercle, that is more or less prominent or acute but apparently ineffective, exists in many of the dynomenids that were examined, such as *D. filholi* Bouvier, 1894, *D. praedator* A. Milne Edwards, 1879, *D. spinosa* Rathbun, 1911, and *D. ursula* Stimpson, 1860. These *Dynomene* species characterized by a sternal differentiation are in contrast to the two preceding *D. tanensis* and *D.* aff. *devaneyi*, as well as to the genera *Acanthodromia* and *Paradynomene*, which have coxal differentiations.

Discussion

It is noteworthy that in certain dynomenids the retaining structure does not involve the limbs any more but takes place on the corresponding somite (sternite 5), certainly a consequence of the broadening of the thoracic plate. Such a difference of position indicates to us that diverse dynomenid crabs belong to distinct genera instead of the traditional single genus *Dynomene*, in other words, that *D. tanensis* and *D.* aff. *devaneyi* must be distinguished in regard to this character and cannot belong to the same genus as the typical species *D. hispida*. It is obvious that in the cases where coxal structures are involved (*Acanthodromia*, *Paradynomene*, *D. tanensis* and *D.* aff. *devaneyi*, Figs 6A-C, 7A-C), the abdomen laterally fills the whole space between the coxae and anteriorly covers a large part of sternite 4. In the case where sternal structures are involved (*Dynomene hispida*, Figs 6D, 7D) the thoracic sternum appears laterally and anteriorly more exposed.

Dynomenids show a pattern like that of dromiids, with an involvement of thoracopods and a major role of P2. No dromiid crab, however, has a structure located on Mxp3 analogous to the configuration in *Acanthodromia*. In regard to dromiids, a dynomenid innovation is, in many of the *Dynomene*, the sternal differentiation on thoracic somite 5, corresponding to P2, just facing the large uropod. The question is to know if the minute structure positioned on the P2 coxa or on sternite 5, that just touches the uropod (perhaps overhanging the uropodal margin in the young individuals) or quite apart in adults, is hence in a position to be effective in retaining. We can assume that, in large males, the abdomen is restricted in its lateral movements. The rudimentary structures, either coxal or sternal, are placed in such a manner that they may fill the same role.

Dynomenids differ from dromiids in many points: in dynomenids the dorsal uropods do not appear to be modified and their sexual dimorphism seems to have no effect; the sexually dimorphic telson never seems to be modified. As homolodromiids and most dromiids, dynomenids have sterno-coxal depressions at the level of P2, P3, and also P4.

The dynomenid apparatus, which disappears in females after the puberty moult, should be studied in detail, especially in living animals during their growth. The examination of the numerous fossil dynomenids would be informative as well. The discovery in ancestral dynomenids of sternal

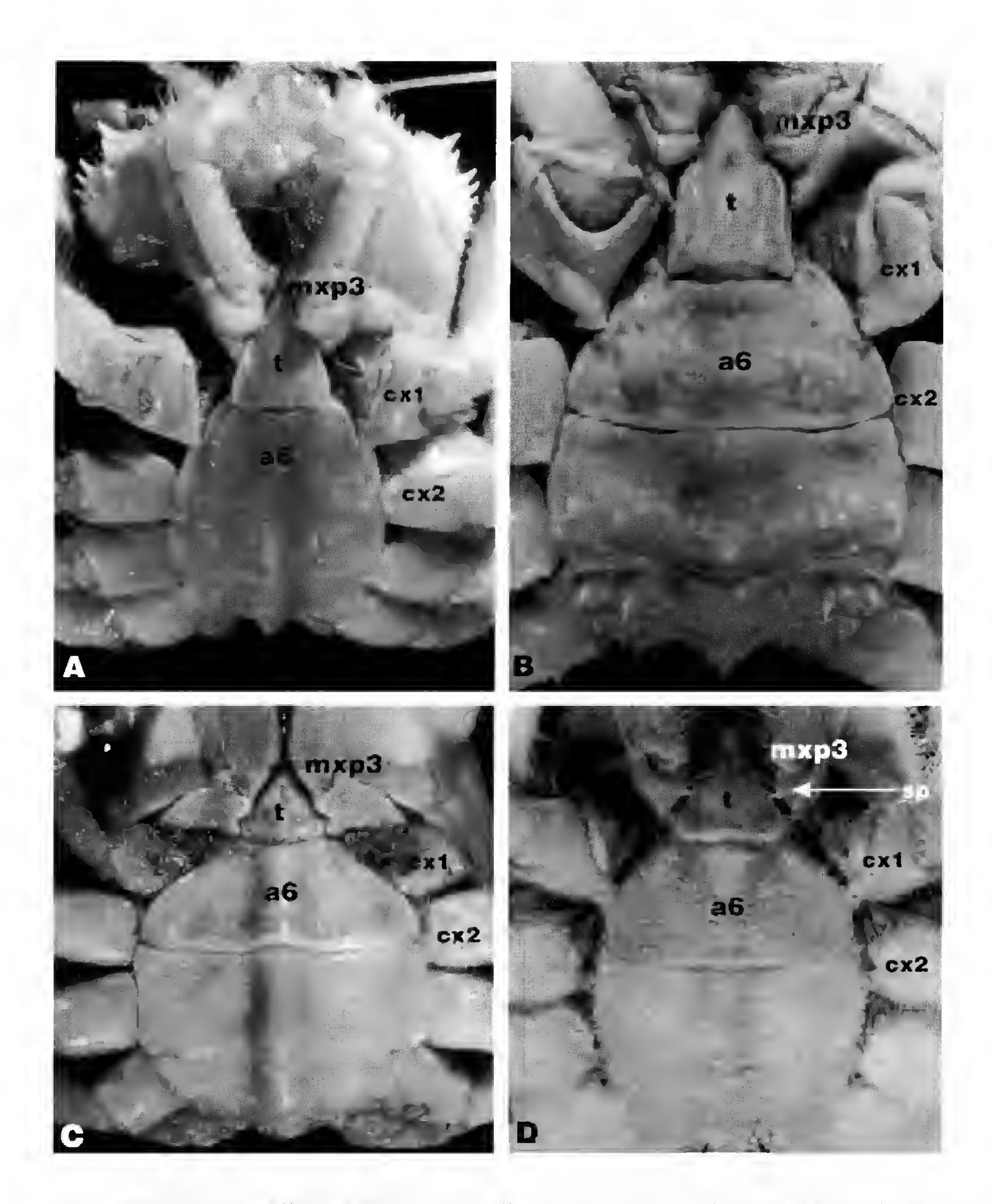


Fig. 8. — Retaining apparatus in Homolidae and Poupiniidae; **A**, *Homola orientalis* Henderson, ♂ 34.8 × 23 mm, French Polynesia (MNHN-B 22385); **B**, *Paromola bathyalis* Guinot *et* Richer de Forges, ♂ 72 × 48 mm, paratype, New Caledonia (MNHN-B 19898); **C**, *Homolomannia sibogae* Ihle, ♂ 39.2 × 27 mm, Philippines, Musorstom 2 (MNHN-B 13825); **D**, *Poupinia hirsuta* Guinot, ♂ 48 × 38 mm, holotype, French Polynesia (MNHN-B 24346). Abbreviations: **a6**, abdominal segment 6; **cx1**, **cx2**, coxae of P1, P2; **mxp3**, external maxilliped; **sp**, spine; **t**, telson.

TABLE 1. — Diagramatic representation of various modes of abdominal holding. (In white: articles of appendages involved; stippled zone: abdominal part; in grey: sternal somite 4). **A**, simple juxtaposition without any differentiation nor projection; **B**, juxtaposition by a projection, without a notch on abdomen; **C**, coaptation by engagement involving a differentiated structure together with a notch on abdomen, **D-F**, various modes of overhanging; **G**, **H**, overhanging and coaptation by engagement; **I**, coaptation by engagement involving a differentiated structure together with a notch on abdomen; **J**, juxtaposition by a differentiated structure, without a notch on abdomen. The homolid press-button (coaptation by assemblage), present in all genera, is represented by fig. **K**.

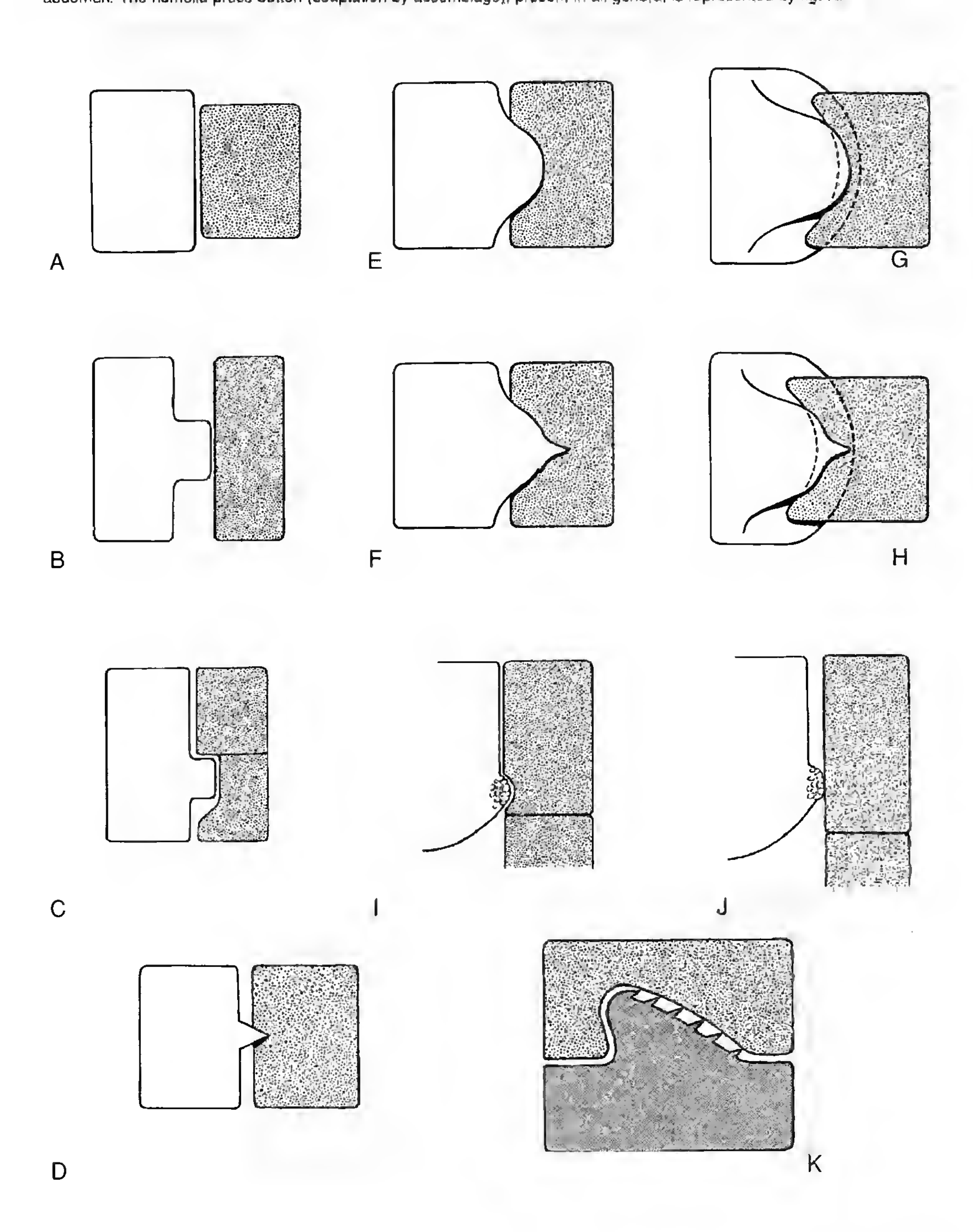


TABLE 2. — Modes of abdominal holding and various involved appendages in the genera of the family Homolidae. Letters refer to table 1. The shape of the differentiated structures (spine, granule, tubercle, or others) was not given. Letters in brackets indicate a nonfunctional structure. The coxa often has two distinct zones that may show a different mode of retaining. (Data for the genus *Gordonopsis* are from Guinot & Richer de Forges 1995).

	Thoracopods						
GENUS	Mxp2	Mxp3 articles			coxae of		
	coxae	coxae	basis	ischion	P1	P2	P3
Homola		H			D	D	D
Paromolopsis		(J)-D	E		J	J	(J)
Paromola		I-H	E		D	D	D
Moloha		I-F	F		D	I	I
Latreillopsis		I-F	F	D	J	(J)	(J)
Dagnaudus	A	B-D	I		C	I	I
Ilhopsis		I-G	E	D	E	A	A
Homolochunia		I-F	F	(E)	E	(A)	(A)
Yaldwynopsis		I-D		I	I	I	I
Hypsophrys	A	J-H			I-E	I	I
Gordonopsis	?	?	?	?	I	I	(I)
Homologenus		C			F	(D)	(D)
Homolomannia	A	C-G	E	E	E	(A)	(A)
Homolax	A	J-D	D		J-A	J	J

prominences used as projections overhanging the uropods, instead of the acanthodromiid, paradynomenid and (*pro parte*) dynomenid coxal projections, would be very significant.

SUPERFAMILY HOMOLOIDEA de Haan, 1839

The superfamily Homoloidea has long been associated with the Dromiacea, and certain authors (Hartnoll 1975; Stevcic 1981; Bishop 1986) have continued to subordinate Homoloidea to the Dromiacea. But, at the present time, the morphological and spermatological data support the proposition that the Homoloidea should be removed from the Dromiacea and, at a higher level, their inclusion in a single grouping, the Podotremata (Guinot *et al.* 1994; Guinot & Richer de Forges 1995). Before the establishment of the Poupiniidae, the Homoloidea were characterized as having the P5 dorsal, reduced in length and subchelate or chelate (with the exception of certain latreilliids). Discovery of *Poupinia hirsuta* Guinot 1991, with P5 dorsal and movable, reduced in width but not in length and not subcheliform, changes this definition. In poupiniids the P5 are relatively unmodified but are clearly different from the preceding legs. So the homoloid character of P5 different from P4 (instead of similar P4 and P5 in the Homolodromiidae and most Dromiidae) remains a valuable criterion. The family Homolidae is characterized by a dorsal *linea homolica*, which is absent in the two other families Latreilliidae and Poupiniidae.

FAMILY HOMOLIDAE de Haan, 1839

In homolids the abdomen is long, and the telson engages between the coxae of third maxillipeds and sometimes between second maxillipeds, which in a way clasp the posterior part of the pleon. These crabs are remarkable due to the coexistence of two types of retaining and locking mechanisms (Guinot 1979a; Guinot & Richer de Forges 1995). On the one hand, a retaining system: several projections on the coxae of various appendages (Mxp3, P1 through P3) are involved, often acting simultaneously (Tables 1, 2). On the other hand, a locking mechanism: differentiated structures are present on the sternal surface, with a pair of special prominences (on sternite 4) fitting into a pair of sockets in the internal part of the abdominal segment 6.

Structures on appendages

Most homolids immobilize their abdomen by using either a deep depression on the coxae that

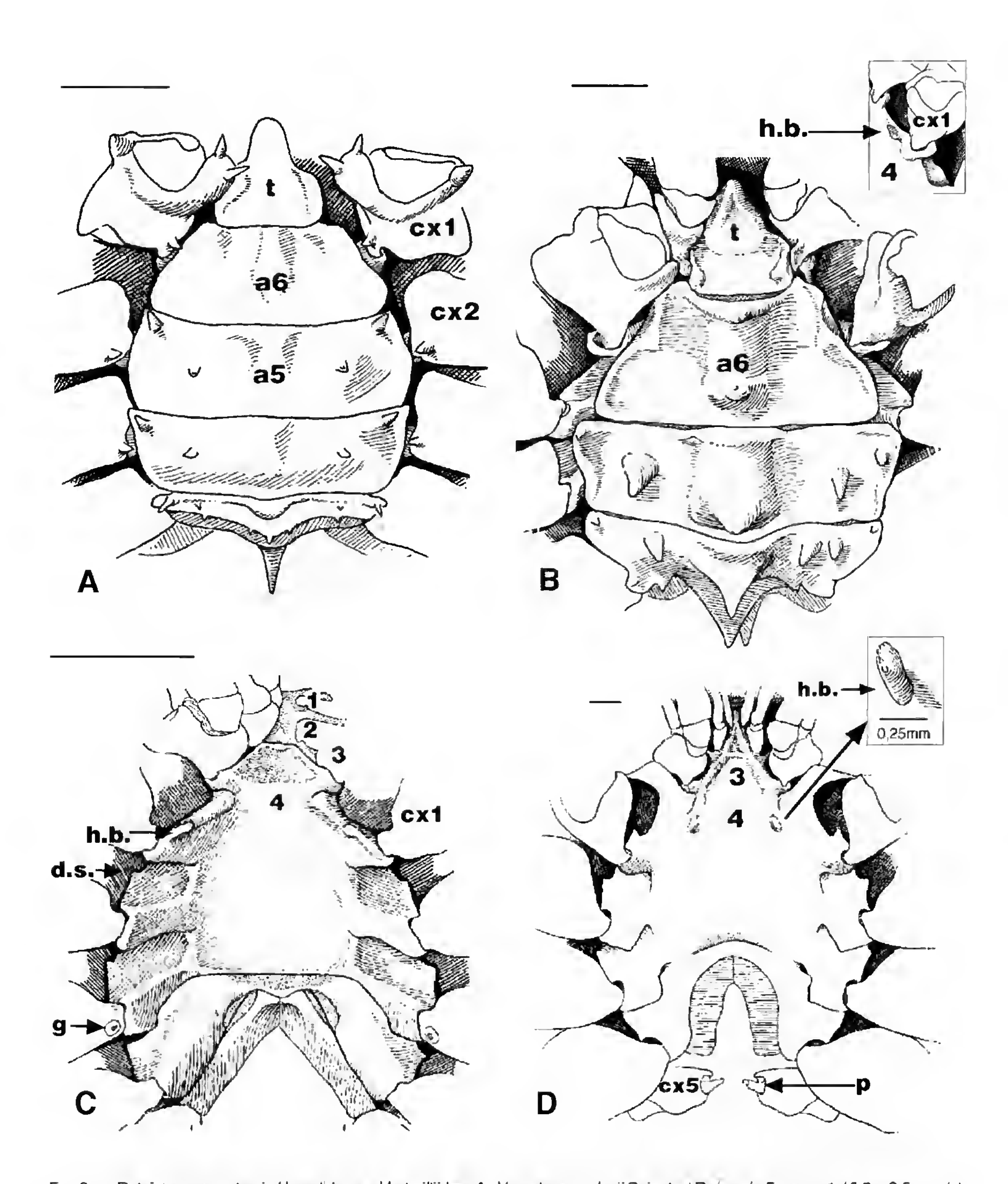


FIG. 9. — Retaining apparatus in Homolidae and Latreilliidae; **A**, *Homologenus levii* Guinot *et* Richer de Forges, ♂ 10.2 × 6.5 mm (cl without rostrum, cw without lateral spines), paratype, Chesterfield Islands (MNHN-B 19883). **B**, *Homolochunia kullar* Griffin *et* Brown, ♂ 26.5 × 23 mm (cl without rostrum), New Caledonia (MNHN-B 16662), with detail of cx1 and homolid press-button; **C**, *Homola ranunculus* Guinot *et* Richer de Forges, ♂ 42.6 × 35.5 mm, paratype, New Caledonia (MNHN-B 20272); **D**, *Latreillia* aff. *valida* de Haan, ♂ 13.5 × 8.3 mm, New Caledonia, Halipro 1, stn CP 851 (MNHN), with detail of the homolid press-button. Abbreviations: **a5**, **a6**, abdominal segments 5, 6; **cx1**, **cx2**, **cx5**, coxae of P1, P2, P5; **d.s.**, sterno-coxal depression; **g**, female gonopore; **h.b.**, homolid button; **p**, penis; **t**, telson; **1**, **2**, **3**, **4**, sternites 1-4. Setae were not figured. Scale bars: A, C, 5 mm; B, D, 1 mm.

corresponds with complementary surfaces on the abdominal margin, or diverse structures (such as granules, tubercles, spines, spinules, groups of similar structures, or a sliding surface). The structure situated on the coxae of Mxp3 correspond to the posterior part of telson, those on P1 coxae to abdominal segment 6, those on P2 coxae to abdominal segment 5, and those on P3 coxae (a structure probably nonfunctional) to abdominal segment 4, respectively. These structures may fit into complementary parts of the abdomen or overhang it. Tables 1 and 2 summarize the action of the various appendages involved, with their respective modes of coaptation.

Some examples are briefly reviewed here.

In *Homologenus* A. Milne Edwards, 1888 (Fig. 9A), probably very primitive, the extremity of the telson engages between the bases of the Mxp3, which props up. In addition, a remarkably long and spinose prominence on P1 coxa completely overhangs the telson. The spines on P2 and P3 coxae seem ineffective. In *Lamoha* Ng, 1998 (= *Hypsophrys* Wood-Mason, 1892) the telson is propped up by Mxp2, overhung by Mxp3,

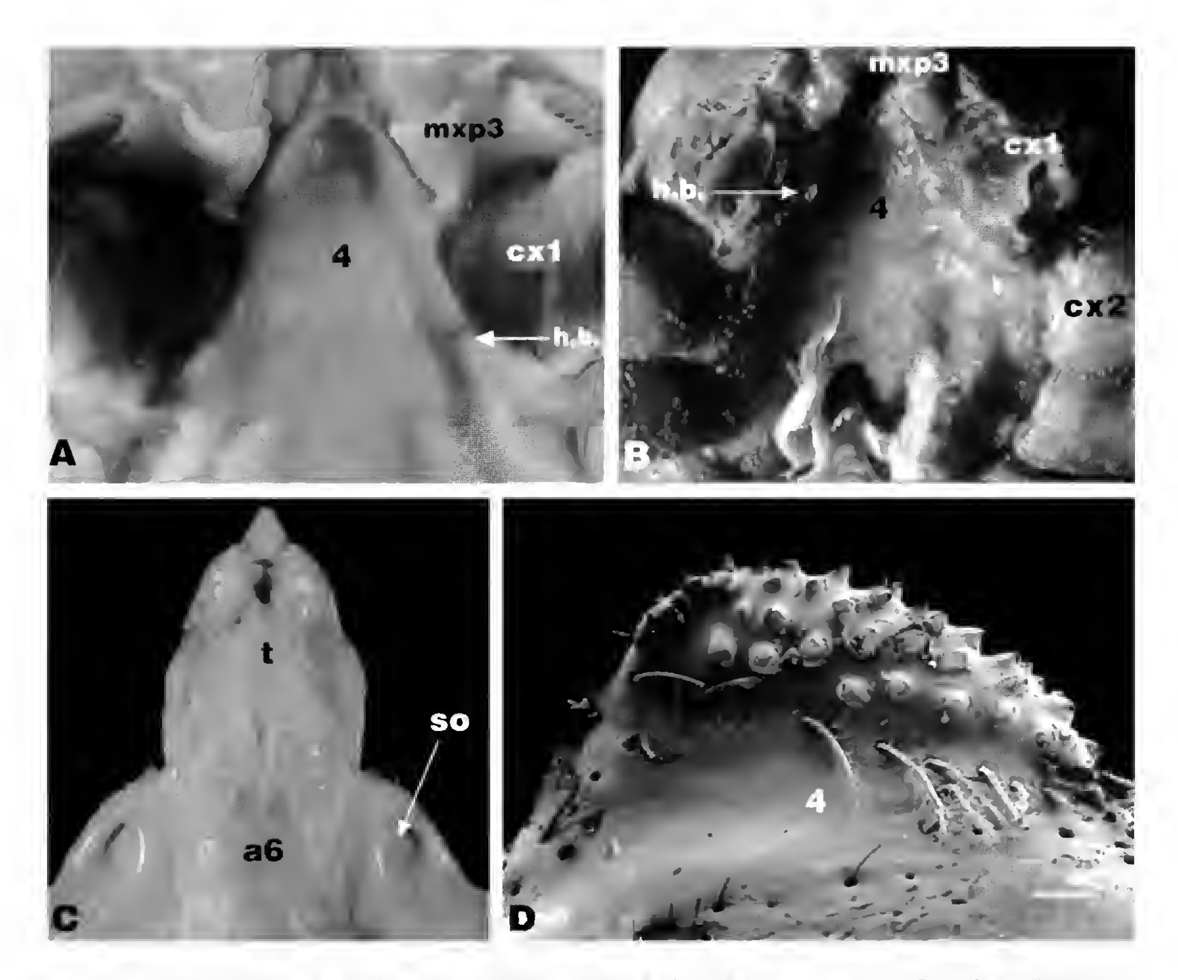


FIG. 10. — Homolid button and socket in Homolidae and Latreilliidae; **A**, **C**, *Moloha majora* (Kubo), ♂ 51 × 38 mm, Sagami Bay (MNHN-B 24798); **A**, thoracic sternum without abdomen, **C**, ventral surface of abdomen; **B**, *Latreillia valida* de Haan, cl 16 mm, Japan (MNHN): thoracic sternum without abdomen; **D**, *Homola orientalis* Henderson, ♂ 31.6 × 25.2 mm, French Polynesia (MNHN-B 22385): photographs with the scanning electron microscope of the right homolid button, internal side view. Abbreviations: **a6**, abdominal segment 6; **cx1**, **cx2**, coxae of P1, P2; **h.b.**, homolid button; **mxp3**, external maxilliped; **so**, socket; **t**, telson; **4**, sternite 4. Scale bars: D, 100 µm.

and every articular condyle of P1-P4 (more developed on P1-P2) on the sternum fits on a complementary part of the abdominal margin. *Homolomannia* Ihle, 1912 (Fig. 8C) is characterized by a system that is chiefly provided by the internal margin of the P2 and P3 bases, which cover part of the telson. *Homolochunia* Doflein, 1904 (Fig. 9B), an advanced genus with the last pair of pereiopods terminating in a true subchela (Guinot & Richer de Forges 1981), is characterized by a marked coaptation between the posterior part of the abdomen and the sternum, specially at the level of Mxp3 and P1; the Mxp3 coxa bears a strong projection that fits a complementary part on the telson; an extension of the P1 coxa overhangs pleomere 6; there are no spinules on the other appendages. In *Homola orientalis* Henderson, 1888 (Fig. 8A), *H. ranunculus* Guinot *et* Richer de Forges, 1995 (Fig. 9C) and *Paromola bathyalis* Guinot *et* Richer de Forges, 1995 (Fig. 8B), the appendages involved are similar (Table 2).

Sternal structures

The latero-external borders of the abdomen of homolids reach the proximity of the articular condyles of the coxae of P1 on the corresponding sternite, the sternite 4. In front and very close to this condylus there is a particular sternal structure, very prominent, high, elongated, and not smooth under the binocular; the pair of lateral prominences of somite 4 fits into a pair of sockets hollowed on abdominal segment 6 at its postero-lateral angles [Fig. 10A, C: *Moloha majora* (Kubo, 1936)]. The sternal differentiation appears markedly serrulate, spinulate or tuberculate, with complex microstructures (Fig. 10D) that explain the strength of the locking mechanism.
The abdominal structures of *Homola* were called *crans de rétention* by Pérez (1928b: 649; 1929: 1149). The whole apparatus was named *bouton-pression homolien* (homolid press-button) by Guinot (1978a, 1979a). This paired sternal system, observed in all homolids, latreilliids and poupiniids, appears as a unique innovation of the superfamily Homoloidea.

FAMILY LATREILLIIDAE de Haan, 1840

The sternal plate of latreilliids is broader than in homolids and is not completely covered by the abdomen in males; the telson enters between the bases of maxillipeds. In the few specimens examined, the Mxp3 coxae are never equipped with a spine but, when closed together, seem capable of retaining the telson at its tip. On sternite 4 a pair of very high, cristiform, markedly denticulated and sometimes acute projections, with a complex apical texture, fits into a pair of sockets in the postero-lateral angles of pleomere 6. In the latreilliids in which the sternal plate is only a little broadened, as in *Latreillia valida* de Haan, 1839 (Fig. 10B), the sternal structure is positioned near the lateral margin of the plate, as observed in the family Homolidae. But in the latreilliids in which a larger part of the thoracic sternum becomes laterally exposed and with a broad sternite 4 extended in front of chelipeds, the sternal structures protude nearer the medial part of the plate (Fig. 9D; see also *Latreillia manningi* Williams, 1982, fig. 2d). It is noteworthy that the sterno-coxal depressions are completely absent in all latreilliids.
The family Latreilliidae has the same press-button apparatus as the family Homolidae. The homolid press-button seems to remain the only effective mechanism in latreilliids: the bases of the pereiopods, far from the abdominal margins, are unused. The press-button in latreilliids proves to be very effective, and it is definite that the surface of the denticulated button possess microstructures that improve the mechanism.

FAMILY POUPINIIDAE Guinot, 1991

Males and females of *Poupinia hirsuta* Guinot, 1991 bear two kinds of systems, on limbs and on the sternum, which apparently operate simultaneously (Fig. 8D).
Two very acute spines project from the coxa of Mxp3 and clearly overhang the telson, which penetrates far between the maxilliped bases. These spines are truly effective but require that the Mxp3 move close together. A spinule located at the base of the P1 coxa, however, appears insufficient to be operative. A pair of ornamented sternal prominences lies on the sternal plate (sternite 4), near the articulation with chelipeds and fits into a pair of deep sockets hollowed on the internal surface of abdominal segment 6.

The poupiniids, distinctive because of their ovoid carapace, their P5 not adapted for carrying behaviour or for grasping, and their high gill count, possess the same "homolid press-button" as homolids and latreilliids.

Discussion

Projections on the basal parts of appendages are used in homolids (on Mxp3 and P1 through P3) and poupiniids (on Mxp3), together with the homolid press-button. In latreilliids, in which the sternum is broadened, only the carinate and setrulate prominence on sternite 4 seems to be used. A significant result of our investigations is that the "homolid press-button" represents a synapomorphy for the homoloids, supporting the inclusion of Homolidae, Latreilliidae and Poupiniidae in the same group, the Homoloidea. As a structure, situated on the sternal plate, and as a mechanism, the "homolid press-button" is similar to the typical press-button in eubrachyuran crabs which is always found on sternite 5, instead of sternite 4 as in homoloids. We agree with Pérez (1928b, 1929) who concluded that *Homola* cannot represent the passage between dromiids and true Brachyura, despite the fact that the socket occupies the same pleomere, the sixth, as in the Heterotremata-Thoracotremata assemblage.

Similar to the Dromiacea, homolids and poupiniids have deep sterno-coxal depressions inside which the P2 and P3 coxae may slide. For us, absence of sterno-coxal depressions in latreilliids, which present more advanced features (especially along with a wider sternum) than homolids and poupiniids, might be correlated with the fact that the pereiopods have no role in abdominal retention.

SUPERFAMILY RANINOIDEA de Haan, 1839

The superfamily Raninoidea, which contains the single family Raninidae, or frog crabs, was subdivided into several subfamilies and assigned to the Podotremata (Guinot 1978a, 1979a, 1993b). The basal relationship of raninoids to the heterotreme-thoracotreme assemblage, indicated by some morphological features, spermatological analysis of *Ranina ranina* (Linné, 1758) (Jamieson 1989) and molecular sequences (Spears *et al.* 1992), was partly refuted by the spermatozoal ultrastructure in two other raninoid taxa (Jamieson *et al.* 1994; Jamieson 1994). The distinctive morphology of the raninoids (elongate body, thoracic pleura largely exposed by reduction of the branchiostegite, elongate and triangular buccal frame, special respiratory apparatus, flattened propodi and dactyli of pereiopods) seems to reflect a high degree of specialization for burrowing, that has characterized the group throughout its long geologic history, since its appearance in the Early Albian.

In raninids the sternal plate is narrow, sometimes linear, and lacks sterno-coxal depressions, while the abdominal segment 6 lacks appendagelike uropods (for the case of the Lyreidinae, see below), the abdomen is very short and only partly and loosely flexed (leaving exposed a large part of the thoracic sternum anteriorly), male pleopods are short, and the P2 through P5 coxae lie close together.

FAMILY RANINIDAE de Haan, 1839

No retaining apparatus was observed in Raninidae except in the subfamily Lyreidinae Guinot, 1993. The extant members of this subfamily are distinguished in particular by an abdomen that flexes segments 4-6 and entirely covers the thoracic sternite 6, and by the thoracic sternum (Guinot 1993b: 1326, 1330, fig. 4). All of the examined representatives of the genera *Lyreidus* de Haan, 1839 and *Lysirude* Goeke, 1986 have a pair of strong elongate projections from sternite 5 ("pterygoid processes" of Bourne 1922) that firmly fits into a pair of deep sockets in the latero-posterior extended angles of abdominal segment 6 (Fig. 11). The base of the projection starts at the level of the articular condylus of P2 on sternite 5. The tip of the projection, more or less strongly recurved and distally hook-shaped, bears an additional subdistal hook. The whole structure acts as a safety catch. The configuration may remain effective in ovigerous females, even with a large egg mass: the projections are always present, but the hooks become more or less blunt.

In *Lyreidus brevifrons* T. Sakai, 1937 (Fig. 11A, B) the apparatus is somewhat similar to that of *L. tridentatus* de Haan, 1841 (Guinot 1979a: 128, pl. 22, figs 6, 7; 1993, figs 6, 7). In *L. ste-*

nops Wood-Mason, 1887, the projection also ends in two hooks, distal and subdistal, similar to those of *L. brevifrons* and *L. tridentatus*. A mature female, however, from the Philippines (36.4 × 21.9 mm, Musorstom 1980, stn 71) identified by G. D. Goeke as *L. stenops*, was observed with two subdistal hooks in addition to the distal hooked-tip.

In *Lysirude*, at least in *L. channeri* (Wood-Mason, 1885), the sternal projection is shorter than in the examined *Lyreidus* species. It lies entirely on the sternal surface. In juvenile females and adult males of *Lysirude channeri* (Fig. 11C) the projection is lifted up at the hooked tip and bears a subdistal hook, giving an effective locking mechanism. In mature females (Fig. 11D) the projection becomes entirely applied on the sternal surface and becomes gradually smooth (sometimes except for a small denticle) and more setose with size. The abdominal socket is obsolete or absent, and locking is no longer possible.

Feldmann & Wilson (1988: 478) noticed that "the males, in mature Recent species of *Lyreidus* and *Lysirude*, possess straight bladed, raised flanges; whereas the female possesses notably reduced, outwardly curved projections". We observed that the locking apparatus is sexually dimorphic in *Lysirude channeri*, but not so clearly in *Lyreidus* species that were examined. The dimorphic state noted by T. Sakai (1937: 170) in *Lyreidus tridentatus* concerns abdominal segment 5 and not the thoracic sternite 5 (see Feldmann & Wilson 1988).

Discussion

Only in *Lyreidus* and *Lysirude* is the abdomen situated between P3-P4, fixed against the ventral surface, and pleomere 6 bears a socket. The differentiation which ensures retention is located on sternite 5, as the prominence in certain advanced dynomenids (Figs 6D, 7D) and the typical press-button of eubrachyran crabs (see Figs 13-17, 20-24).

A complete re-examination of all the fossil raninoids, which diversified in the Cretaceous and flourished in the Eocene, should enable further resolution of the abdominal holding apparatus, especially with the examination of the lyreidines. On the preserved sternal plate the processes arising from sternite 5 and the presence of hooks must be checked in fossil crabs attributed to *Lyreidus* (*L. succedanus* Collins *et* Rasmussen, 1992, *L. rosenkrantzi* Collins *et* Rasmussen, 1992, and *L. bispinulatus* Collins *et* Rasmussen, 1992, all from Upper Cretaceous-Lower Tertiary from West Greenland). *Rogeus orri* Berglund *et* Feldmann, 1989, from Lower Middle Eocene of Oregon, distinctly shows a pair of projections: we wonder whether they played a similar role to that in extant Lyreidinae. The precise configuration of processes arising from sternite 5 would be noted in another fossil raninoid subfamily, the Palaeocorystinae Lörenthey *in* Lörenthey & Beurlen, 1929, especially in *Notopocorystes* McCoy, 1849, the oldest known genus of the superfamily Raninoidea (Collins 1997).

Superfamily Cyclodorippoidea Ortmann, 1892

We use this category for convenience to regroup the families, Cyclodorippidae, Cymonomidae and Phyllotymolinidae, despite possible paraphyly (M. Tavares pers. com.). As in Homoloidea and Raninoidea (and all Eubrachyura) pleomeres 3-5 lack vestigial pleopods, and abdominal segment 6 lacks (dorsal or lobiform) uropods. A character shared by all Cyclodorippoidea is the wide sternal plate. For each pair of pereiopods the respective bases of the coxae are very far apart so that there is no contact between the margin of the abdomen and the bases of the legs. A very short and more or less excavated sterno-abdominal cavity is present, with its complete space occupied by stout pleopods. Complementary parts between the borders of both this cavity and the abdomen secure it in place. Additionally, a peculiar holding may occur, that is different in the families Cyclodorippidae and Phyllotymolinidae.

Family Cyclodorippidae Ortmann, 1892

A sterno-abdominal cavity, which is deeply hollowed but very short, is characteristic of the family since it occupies only the posterior part of the thoracic sternum (sternites 6-8). The short abdomen, characterized by the presence of a long pleotelson, is bent at right angles, its posterior half being applied against the sternal surface. In addition, at the level of sternite 6, the lateral border of

the cavity is marked by a groove into which the thin borders of the pleotelson can engage by moving forward. It was named "sliding system" (*système à glissière*) by Tavares [(1994: 210; 1996, fig. 9A-C, E; 1998: 116, figs 7A-C, 8 for *Clythrocerus nitidus* (A. Milne Edwards, 1880)]. There is a coaptation by engagement of the borders of both sternum and pleotelson, but without any sockets.

FAMILY PHYLLOTYMOLINIDAE Tavares, 1998

There is a relatively shallow sterno-abdominal cavity, without well-defined borders. The abdomen is short, the telson only reaching somite 5. The sternite 6 bears a pair of oblique prominences in *Phyllotymolinum* Tavares, 1993 and a pair of granular ridges in *Genkaia* Miyake *et* Takeda, 1970, structures with which the enlarged base of the telson forms a block system, named

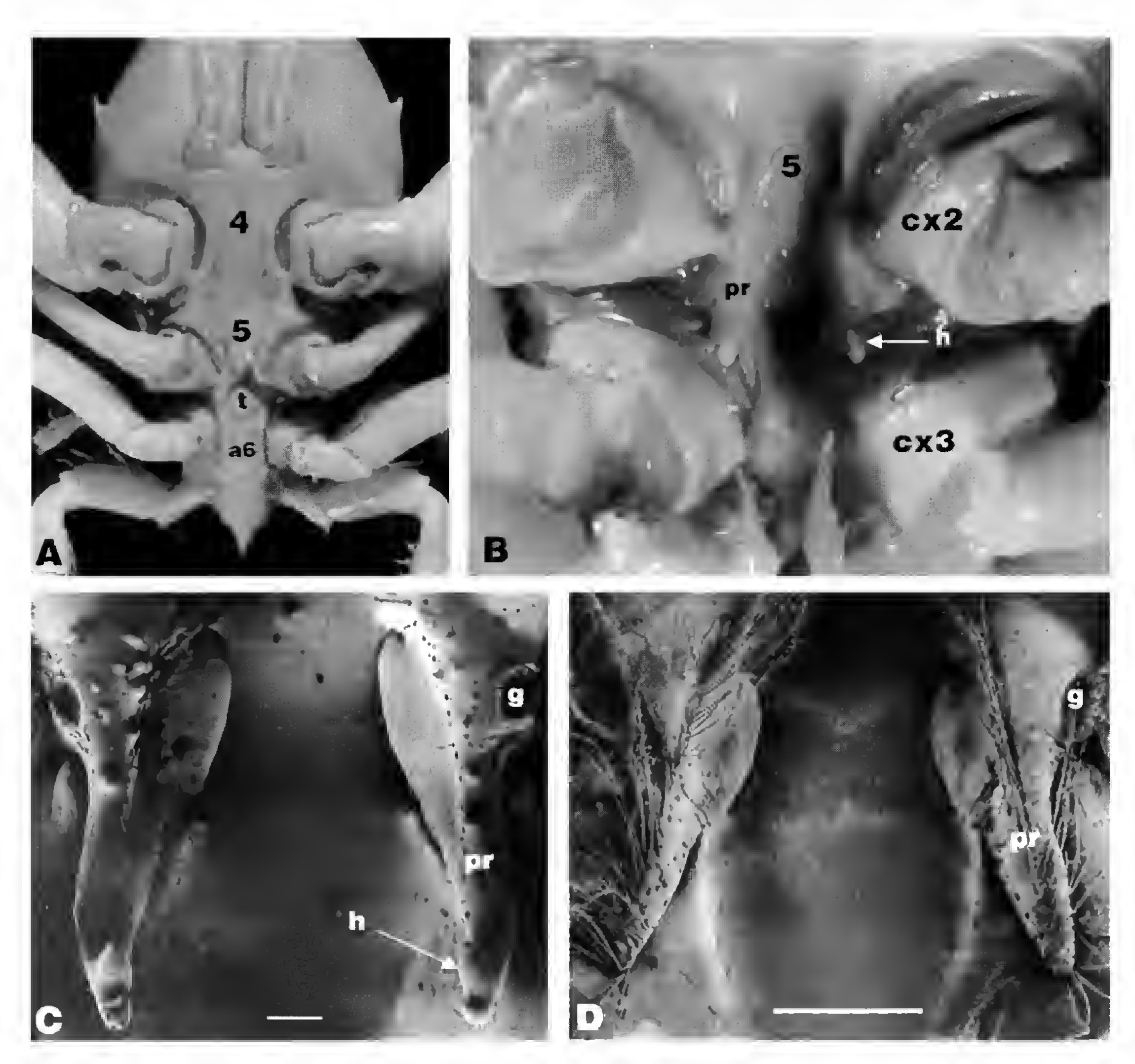


FIG. 11. — Locking apparatus in Lyreidinae (Raninidae); **A**, **B**, *Lyreidus brevifrons* T. Sakai, ♂ 49.4 × 23.4 mm, New Caledonia (MNHN-B 24319): **A**, ventral surface with abdomen flexed in locking position; **B**, without abdomen; **C**, **D**, *Lysirude channeri* (Wood-Mason), Philippines (MNHN-B 11562), **C**, ♂ 25.5 × 17.4 mm; **D**, ♀ 33.7 × 20.5 mm: photographs with the scanning electron microscope to show the pairs of projections with hooks well developed in a male, blunt or lost in an old female. Abbreviations: **a6**, abdominal segment 6; **cx2**, **cx3**, coxae of P2, P3; **g**, ginglymus for articular condylus of P2; **h**, hook; **pr**, projection with hooks; **t**, telson; **4**, **5**, sternites 4, 5. Scale bars: C, 100 µm; D, 1 mm.

système à butoir by Tavares (1994: 208, 209; 1998: 116, fig. 1B).

Family Cymonomidae Bouvier, 1897

There is only a shallow sterno-abdominal cavity, the sternites 6-8 being only slightly concave, and the abdomen is very short. No special structure for abdominal holding was observed (Tavares 1994). As in the Cyclodorippidae, the abdomen is bent in its middle at right angles forming two sections. The posterior pleomeres thus remain completely applied against the sternum (M. Tavares pers. com.). It is reminescent of the cases of *Hypoconcha arcuata* and *H. panamensis* in which the abdomen is bent at right angles in the posterior part of segment 5 (Fig. 1D).

Discussion

The two retaining systems found in the cyclodorippids (coaptation by engagement) and phyllotymolinids (block system) were one character used in the cladistic analysis by Tavares (1994) that allowed the erection of the Phyllotymolinidae as a new family (Tavares 1998).

In contrast to all Podotremata previously mentioned, in the Cyclodorippoidea the sternal plate has acquired a "normal" width and is grooved by a true sterno-abdominal cavity: the coxae of the appendages cannot be involved in the retention, and sterno-coxal depressions are absent. In the Cyclodorippidae there is a coaptation by engagement, whereas in Phyllotymolinidae an innovation is the emergence of a pair of prominent sternal structures (on sternite 6, a very posterior sternite). In both cases no corresponding sockets exist on abdomen and it is only the telson which is involved by slipping along the sternal grooves (Cyclodorippidae) or by blocking at the sternal prominences (Phyllotymolinidae).

Superfamily Dakoticancroidea Rathbun, 1917

Family Dakoticancridae Rathbun, 1917

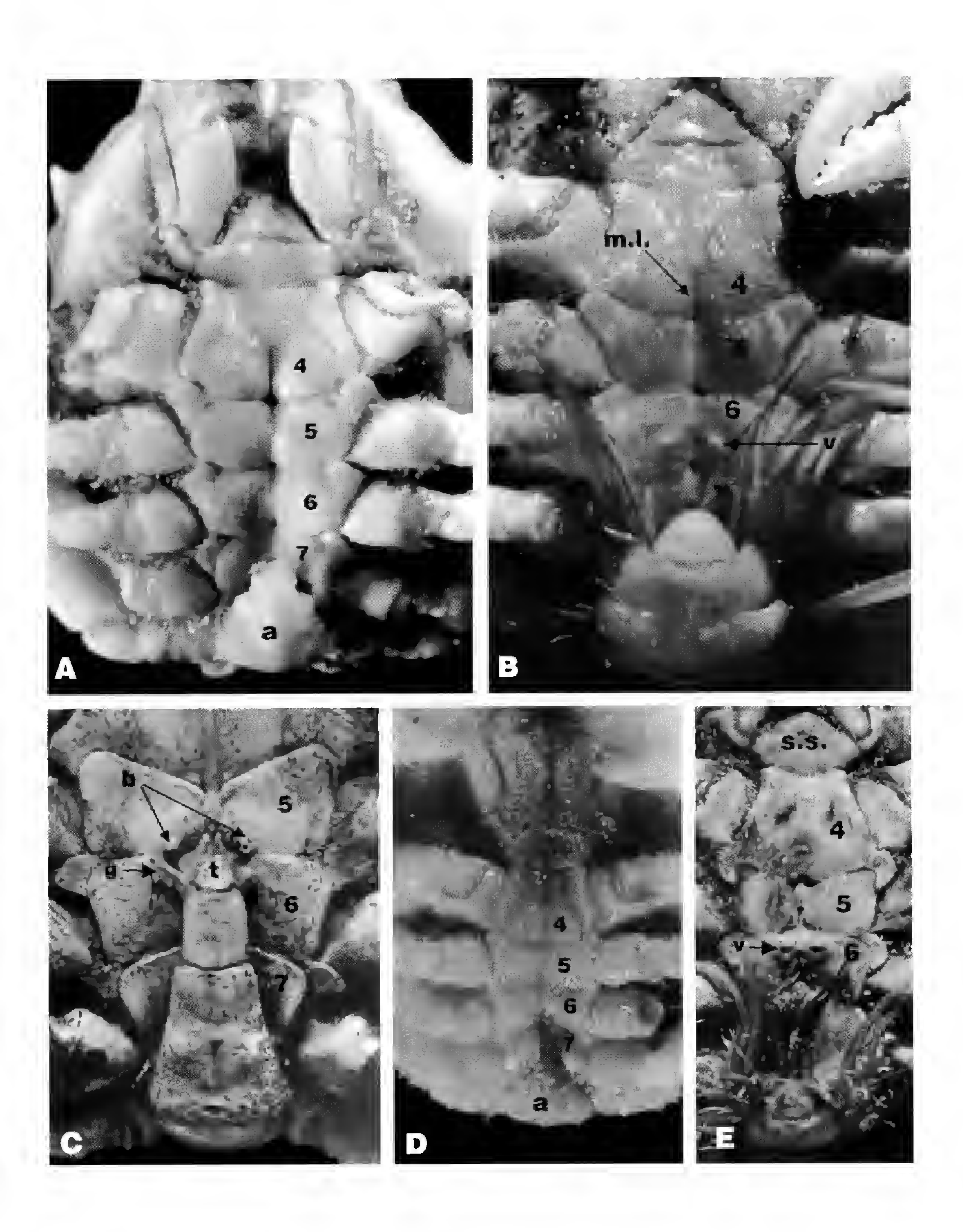
The exclusively fossil family Dakoticancridae, from the Cretaceous of North America, was confirmed as belonging in Podotremata because of the large spermathecal orifices accompanying the coxal female gonopores on P3 (Guinot 1993b). The dakoticancrids have a very broad thoracic sternum, an abdomen without uropods (at least in dorsal view), and a well-excavated sterno-abdominal cavity. On sternite 5, along the border of this cavity, a set of granules was observed at the level of abdominal segment 6, but rather similar to that on the following sternites (*ibid.*, figs 6, 8): their role in abdomen holding is questionable.

HETEROTREMATA Guinot, 1977

The Heterotremata and Thoracotremata share a sternal location of the female gonopores, with the innovation of the vulvae opening on sternite 6 in direct communication with the seminal receptacle. There is now only one female orifice for reproduction. Another strong synapomorphy of the heterotreme-thoracotreme assemblage is the morphology of the first male pleopod, which is completely closed and provided with two distinct basal foramina for the introduction of the penis and the second gonopod (Guinot 1979a: 239). The monophyly of the non-podotreme brachyurans is well supported.

The Heterotremata generally show a coxal location of the male gonopores on the P5 coxae. But members of some families (in the Dorippidae, diverse Dorippinae and all Ethusinae, and members of the Leucosiidae and Goneplacidae) and certain advanced heterotreme families (Hymenosomatidae, Pinnotheridae, Cryptochiridae) exhibit a coxo-sternal organization with the penis located in a sternal groove or potential channel, and embedded under the sternal plates (Guinot & Richer de Forges 1997). This requires providing a more precise definition of the Heterotremata, in contrast to the Thoraco-

Fig. 12. — Configuration of ventral surface in the Corystidae; **A**, **B**, *Corystes cassivelaunus* (Pennant); **A**, ♂ 35.2 × 24.6 mm, Bay of Biscay (MNHN-B 5381): buttons absent; **B**, ♀ 31 × 24 mm, East Channel (MNHN-B 5385): vulvae not covered by abdomen; **C**, *Nautilocorystes ocellatus* (Gray), ♂ 39.5 × 34 mm, Cape of Good Hope (MNHN-B 3924S): buttons present (broken on one side) but far from pleomere 6. **D**, *Gomeza bicornis* Gray, ♂ 26 × 21.3 mm, Moluccas (MNHN-B 17168): note the very short abdomen; **E**, *Pseudocorystes sicarius* (Poeppig), ♂ 50 × 44 mm, Chile (MNHN-B 5407): vulvae not covered by abdomen. Abbreviations: **a**, abdomen; **b**, button of the press-button; **g**, G1; **m.l.**, median line; **s.s.**, sternal shield (sternites 1-3), **t**, telson; **v**, vulva; **4**, **5**, **6**, **7**, sternites 4-7.


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tremata, which attempts a better distinction concerning the patterns for male ducts.

FAMILY CORYSTIDAE Samouelle, 1819

In *Corystes* Bosc, 1802, with a narrow, rather flat and horizontally metamerized thoracic sternum (Guinot 1979a: 81, 132, pl. 9, fig. 1), and in *Pseudocorystes* H. Milne Edwards, 1837 (Guinot 1979a: 132, fig. 20B) the bottom of the sternal plate is longitudinally divided by the median line, which is complete from the sternites 4 through 7 (*Corystes*, Fig. 12A, B), or interrupted (*Pseudocorystes*, Fig. 12E). There is an undefined sterno-abdominal cavity. The male abdomen is very short and has the two first pleomeres in a dorsal position; its pleomere 6 lies posteriorly and does not go beyond sternite 7. Retaining structures are absent in all specimens examined. Abdominal sexual dimorphism is weak. It is noteworthy that in these two genera the vulvae remain uncovered by the abdomen which is very short, even in females. Exposed vulvae (Fig. 12B, E) are rarely observed in brachyuran crabs (Guinot 1979a, pl. 25, figs 4-6).

In *Gomeza* Gray, 1831 the sternal plate is very narrow, well metamerized and longitudinally grooved by the median line that extends from sternites 4 through 8, and the sterno-abdominal cavity occupies a posterior location, being excavated only on sternites 7 (partly) and 8. The abdomen is very short. It is only a tuft of long and stiff setae from the small telson, which helps close the posterior part of the cavity and shelters the sexual pleopods. In *G. bicornis* Gray, 1831 (Fig. 12D) the abdomen is special, with the somites laterally expanded (as with pleural prolongations). At the level of somite 6, the lateral part bends vertically and closes the cavity on each side. Structures of the press-button type are absent. In females of *Gomeza* the abdomen remains very short and laterally expanded, there is no true sterno-abdominal cavity (only a lowering of the somites) and the vulvae cannot be covered by the telson, which lies far backwards. The egg mass is unprotected.

The configuration in *Jonas* Jacquinot *et* Lucas, 1853 is similar, with a relatively short abdomen. The long first pleopods, however, are exposed in grooves of the sternal plate, outside the sterno-abdominal cavity. Only a damaged male specimen of *J. distincta* (de Haan, 1835) was examined, and no locking structures were observed.

Only two incomplete males (a subadult and an adult with a damaged abdomen) and a juvenile belonging to the genus *Nautilocorystes* H. Milne Edwards, 1837 (Guinot 1979a: 133, fig. 20C, pl. 23, fig. 5) were examined. Its general organization (Fig. 12C) is similar to the preceding genera: a sternal plate horizontally metamerized and longitudinally grooved, and an undefined sterno-abdominal cavity. In comparison to *Corystes*, the abdomen is longer, but the postero-lateral angles of pleomere 6 remain far from sternal suture 5/6. A pair of acute, reversed hooks is positioned at the base of sternite 5, very close to suture 5/6. No sockets on the pleomere 6 could be observed. There is such a large gap between the sternal hooks and any part of pleomere 6 that contact appears impossible.

FAMILY ATELECYCLIDAE Ortmann, 1893

Rice (1981a) suggested that the family Atelecyclidae *sensu lato* was not a monophyletic group.

Atelecyclus Leach, 1814 (Guinot 1979a: 136, pl. 9, figs 4, 5, pl. 23, fig. 9) has a very narrow and medially grooved sternal plate and a weakly hollowed sterno-abdominal cavity. Both parts of the press-button system are present and functional. In juveniles and adult males (up to about 46 × 47 mm; fifteen specimens examined) of *Atelecyclus rotundatus* (Olivi, 1792) the developed tubercles and sockets form an effective locking mechanism. In the same sample that was examined from the Bay of Biscay, a male (35.4 × 36.8 mm; Fig. 13A) was found with the two complementary parts firmly assembled, thus an effective locking mechanism; and a slightly smaller male (33.9 × 35.2 mm; Fig. 13B) was found without an effective mechanism, the sockets in the postero-lateral angles of pleomere 6 reaching the suture 5/6 but not the buttons. It looks as if the abdomen is too short in this "abnormal" male.

In *Peltarion* Jacquinot, 1847, about fifty individuals of *P. spinulosum* (White, 1843) were examined. The sterno-abdominal cavity is excavated, and the two parts of the apparatus are well-differentiated. There is a pair of sternal tubercles very close to suture 5/6; sockets are defined on the produced latero-posterior angles of abdominal

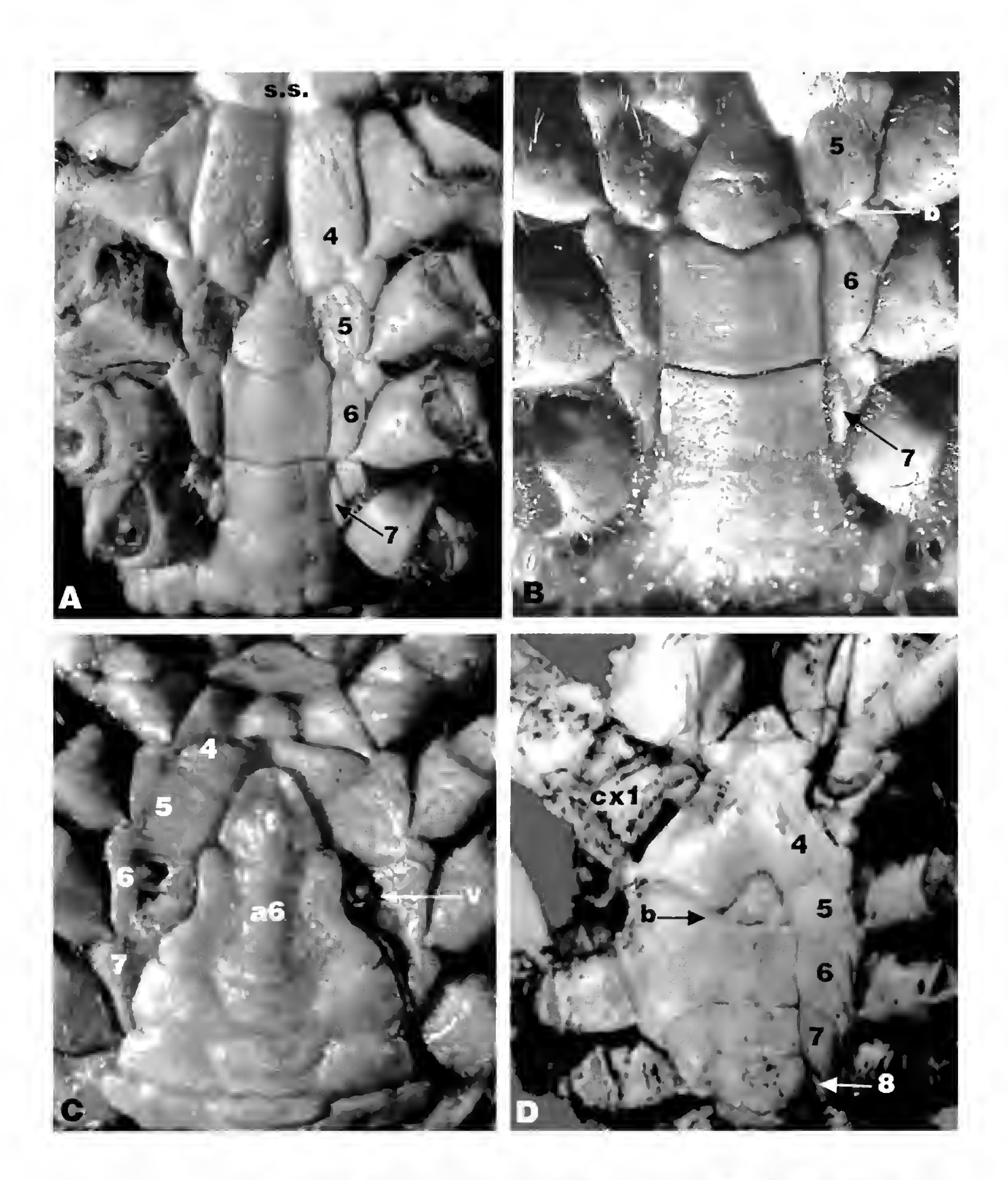


FIG. 13. — Locking apparatus in the Atelecyclidae; **A**, **B**, *Atelecyclus rotundatus* (Olivi), Bay of Biscay (MNHN-B 5400): **A**, ♂ 34 × 35.5 mm: buttons fitting into sockets; **B**, ♂ 33.9 × 35.2 mm: buttons not fitting into sockets; **C**, *Telmessus cheiragonus* (Tilesius), ♀ 35 × 46 mm, Japan (MNHN-B 5408): vulvae not covered by abdomen; note the notch on the edge of pleomere 6, **D**, *Trachycarcinus alcocki* (Doflein), ♂ 70.3 × 65.2 mm, Philippines (MNHN-B 11571): note the bulge on the side of large cheliped and the right button (at left) not fitting into socket. Abbreviations: **a6**, abdominal segment 6; **b**, button of the press-button, **cx1**, coxae of P1; **s.s.**, sternal shield (sternites 1-3); **t**, telson; **v**, vulva; **4**, **5**, **6**, **7**, **8**, sternites 4-8.

segment 6, not very deep, however. Locking is possible but it does not seem very efficient, despite the acuteness of the buttons. In certain males, either small (26.3 × 26.2 mm) or much larger (53.9 × 56.5 mm and 54.8 × 57 mm), there is a small gap between the pair of sternal tubercles and the strongly produced postero-lateral angles of pleomere 6, that is enough to prevent proper fastening. The two components of the locking system are not lost in larger individuals, even if apparently not used. The figure (Fig. 14A) shows a large male individual (54 × 57 mm; cl indicated by error as 52.6 mm in Guinot 1979a: 135, fig. 20D) in which no close connection between the two parts of the apparatus was observed. The size at which the two parts do not attach to each other is variable. In females, the coincidence between the two sternal and abdominal parts exists in some individuals, but the sockets do not seem to be defined. In females from about 32 × 32 mm up, the buttons tend to become smaller and disappear. The material in the MNHN identified as *P. spinulosum* shows a strong variability, notably concerning the areolation and granulation of the dorsal surface of carapace and the spinulation of pereiopods. It would be interesting to verify whether the differences observed in the liaison between the two parts of the locking system might be related to other morphological features. It is noteworthy that *Peltarion* displays various patterns, in particular a non-correspondence even in young males, or an asymmetry illustrated by a larger gap between the two structures on the major cheliped side (a male 41.7 × 43.8 mm).

In *Trachycarcinus* Faxon, 1893, in which one of the chelipeds becomes very large, the pair of tubercles is situated in the middle of sternite 5 and the two components of the apparatus function well. But in two large specimens of *T. alcocki* (Doflein, 1903) (Fig. 13D) and of *T. crosnieri* Guinot, 1986, a non-correspondence was observed on the major cheliped side. The connection only operates on the minor cheliped side. This asymmetry can be explained by the increased development of P1 muscles, which induces a "bulge" of sternite 4 and modifies the general organization of the anterior part of plastron, thus displacing the tubercle on the side in question.

FAMILY CHEIRAGONIDAE Ortmann, 1893
(= TELMESSINAE Guinot, 1977)

A familial rank is provisionally given here to this small group, traditionally assigned to the Atelecyclinae within the family Atelecyclidae, awaiting a revision of all Corystoidea (Balss 1957: 1635; Guinot 1978a: 259; 1979a: 136, pl. 25, figs 1-3; 1989: 349; Rice 1981a: 293; Stevcic 1990: 33; Sasaki & Mihara 1993: 511). The adult and zoeal features of *Erimacrus* Benedict, 1892 and *Telmessus* White, 1846 do not obviously ally them with any known group.

In both *Erimacrus* and *Telmessus*, there is a relatively narrow sternal plate, horizontally metamerized and longitudinally grooved by the medial line, with the buttons (very close to suture 5/6) fitting well into marked sockets. In *T. cheiragonus* (Tilesius, 1812) the large females (for example 35 × 43 mm), with developed pleopods, always have acute buttons corresponding with sockets that remain visible but are partially masked by setae. Most curious is the position of the very wide vulvae lying laterally on the exposed parts of sternite 6, close to the P3 coxae, and appearing even more exposed because of the strong notch on the external margin of pleomere 6 (Fig. 13C).

FAMILY THIIDAE Dana, 1852

The small genus *Thia* Leach, 1815 (for ontogenetic considerations, see Ingle 1984) is characterized by a very narrow, transversally metamerized and longitudinally grooved sternal plate, with a particularly long sternite 4, and by an abdomen that fills the whole space between the legs from P3 through P5, with the telson lying only in a small depression on sternite 5. There is a pair of prominences, with an acute tip, close by suture 5/6. The sockets are shallow but they seem to be effective (Guinot 1979a: 83, 135, 136, fig. 20A).

FAMILY CANCRIDAE Latreille, 1803

The thoracic sternum is not very enlarged in *Cancer* Linné, 1758. All the sutures of the sternum are continuous and parallel, the median line extends until the middle of somite 4, and there is a sterno-abdominal cavity. The button is relatively small but acute, and the socket is deeply

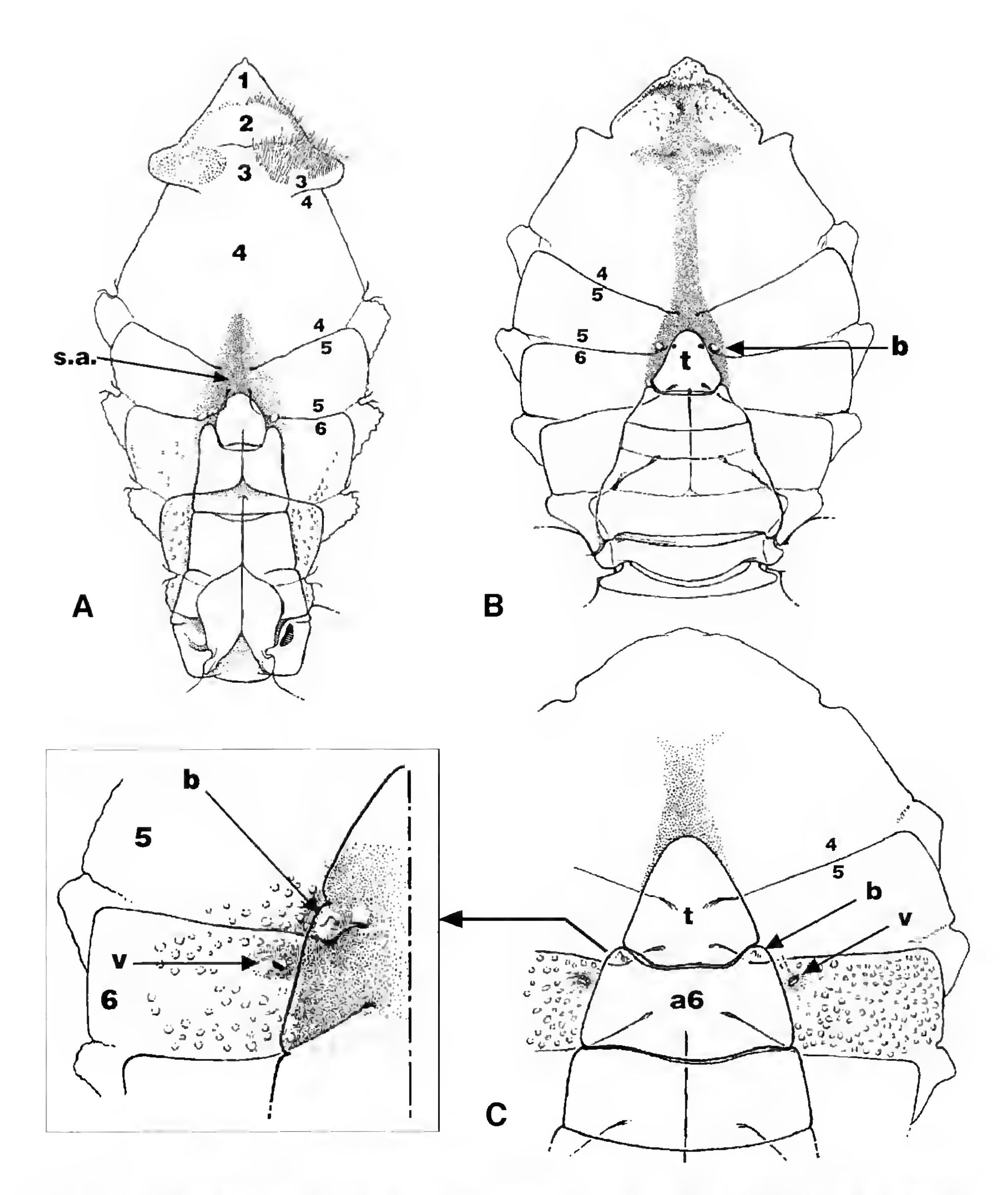


FIG. 14. — Locking apparatus in Atelecyclidae (**A**, *Peltarion* Jacquinot) and Belliidae (**B**, **C**, *Bellia* H. Milne Edwards); **A**, *Peltarion spinulosum* (White), ♂ 54 × 57 mm, Cape Horn (MNHN-B 5405), the two parts of the locking apparatus are not in correspondence, but sternal buttons and sockets are present (After Guinot 1979a, fig. 20C; specimen indicated as cl 52.6 mm); **B**, **C**, *Bellia picta* H. Milne Edwards; **B**, ♂ 50.5 × 45.5 mm, holotype, Peru (MNHN-B 1), thoracic sternum and abdomen, without coincidence between the buttons and the sixth abdominal segment; **C**, ♀ 29 × 25.4 mm, "Tahiti" (erroneous origin) (MNHN-B 2); note in this young female the coincidence between the buttons and the sixth abdominal segment, and buttons located close to the exposed vulvae. Abbreviations: **a6**, abdominal segment 6; **b**, button; **s.a.**, sterno-abdominal cavity, **t**, telson, **v**, vulva; **1-6**, sternites 1 through 6; **3/4**, **4/5**, **5/6**, sternal sutures 3/4, 4/5 and 5/6. The parts located under abdomen are drawn with a continuous line. Setae were not figured.

hollowed and lined by a thick ridge on the postero-lateral angles of pleomere 6.

FAMILY BELLIIDAE Dana, 1852

In the burrowing *Bellia* H. Milne Edwards, 1848 (Guinot 1976: 48, figs 10B, 11A; 1979a: 134), there is a relatively weak sterno-abdominal cavity. The large holotype of *Bellia picta* H. Milne Edwards, 1848 (male 50.5 × 45.5 mm) (Fig. 14B) bears a pair of small prominences at the posterior part of the sternite near suture 5/6; they cannot be reached, however, by the well-defined sockets of pleomere 6, which lie posteriorly. This would have seemed an aberrant individual but Rathbun (1930: 175, pl. 79, fig. 3) figured the same configuration in a smaller male (cl 28.5; estimated cw 25.3 mm, USNM 22066) in which, there was also no coincidence between the parts, the abdomen looking "too short". In another respect, *B. picta* exhibits a special configuration in females. The vulvae are completely (only partly in small individuals) uncovered by the abdomen and remain exposed on sternite 6, lateral to pleomere 6. In two females (24.8 × 22.3 mm and 29 × 25.4 mm; Fig. 14C) the liaison is normal. But in a large ovigerous female (39.5 × 36 mm) the prominence is replaced with a scar close to the large vulva and the fitting is no more effective (Guinot 1979a, fig. 39A-C). It is noteworthy that the structures lock into each other in a female of cw 22.3 mm but not in a male of cw 25.3 mm, but this can be explained by the markedly short male abdomen in *Bellia picta* (Fig. 14B, C).

In the other genera of the family Belliidae, *Corystoides* Lucas, 1844, *Acanthocyclus* Lucas, 1844 and *Heterozius* A. Milne Edwards, 1867, the few examined specimens show a "normal" configuration as well in the locking apparatus as in the location of vulvae (Guinot 1976: 50-55, figs 10A, C, D, 11B-D; 1979a: 134).

FAMILY ORITHYIIDAE Dana, 1852

Orithyia Fabricius, 1798, monospecific with *O. sinica* (Linné, 1771), was separated from the family Calappidae by Ortmann (1892: 555, 559), who was the first author to suggest a familial status for Orithyiidae within the Calappinea. Alcock (1896: 138) subdivided the Calappinae in two alliances, Calappoida and Orithyioida. Ihle (1918: 178) recognized the relationships linking *Orithyia* to the Dorippidae (better than to the Calappidae). On the basis of the larval stages described by Hong (1976), Rice (1980: 317; 1981a: 293) indicated the presence of a combination of characters unknown in any other identified larvae, although showing some similarities with dorippids, but perhaps "of little significance". For a long time, most carcinologists considered the subfamily Orithyiinae as a component of the Calappidae inside the ancient Oxystomata (Balss 1957: 1611; T. Sakai 1976: 127, 143; Dai & Yang 1991: 101, 113). A separate family, Orithyiidae, distinguished from the Calappidae, was resurrected by Guinot (1978a: 254). Bellwood (1996: 185, fig. 4) defined a clade *Dorippe* + Orithyiinae supported by nine synapomorphies and placed the family inside the Dorippoidea, but many characters, such as those of the abdomen and the vulvae, were not taken into account.

The peculiar configuration of *Orithyia* was described by Guinot (1979a: 133, pl. 14, figs 7-9) despite poor and incomplete material. It is now possible to document this with additional specimens. The thoracic sternum is very wide and circular, with all the sutures interrupted and the presence of a medial line on sternites 7 and 8; a large part of sternite 8 is exposed. There is a long sterno-abdominal cavity, its smooth surface contrasting with the granular remainder of the plate. The first two abdominal segments are gathered together between the strong coxae of the subdorsal P5, and pleomere 1 does not seem to be movable. In males, the abdomen is very short and fills only the middle of the sterno-abdominal cavity, its tip not reaching the suture 6/7, and the pleomere 6 lies very far from sternite 5. Neither buttons nor sockets were observed in our large-sized males (Fig. 15A), the short first pleopods of which can be completely sheltered by the abdomen. This observation needs to be verified in young males. In females (Fig. 15B), the abdomen is longer and fills a slightly larger part of the sterno-abdominal cavity, and vulvae are completely external on sternite 6. They remain exposed not because of the abdomen's shortness but because of their lateral location on the plate, outside the cavity.

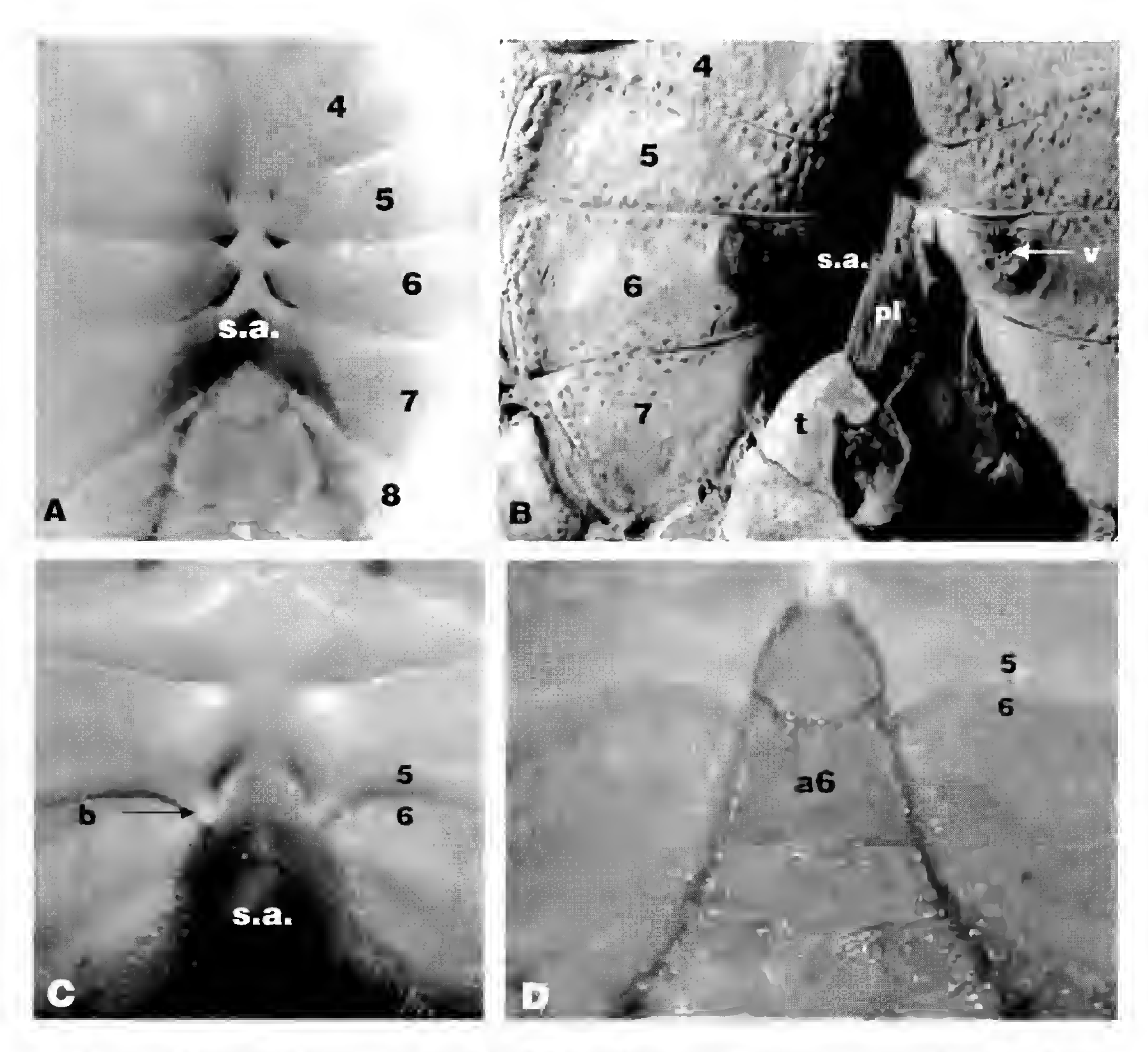


FIG. 15. — Configuration of the ventral surface in Orithyiidae and Dorippidae: A, B, *Orithyia sinica* (Linné); A, ♂ 83.6 × 73.6 mm, China Sea (MNHN-B 11612): sterno-abdominal cavity and very short abdomen; B, ♀ 64 × 60 mm, without origin (MNHN-B 93S): vulvae not covered by abdomen; C, D, *Medorippe lanata* (Linné), ♂ 26.3 × 32.1 mm, Morocco (MNHN-B 19861): C, without abdomen; D, with abdomen in a flexed position. Abbreviations, **a6**, abdominal segment 6; **b**, button of the press-button; **pl**, pleopod; **s.a.**, sterno-abdominal cavity; **t**, telson; **v**, vulva; **5/6**, sternal suture 5/6; **4**, **5**, **6**, **7**, **8**, sternites 4-8.

FAMILY DORIPPIDAE Macleay, 1838

SUBFAMILY DORIPPINAE Macleay, 1838

These Heterotremata are characterized by the last two pairs of legs being dorsal, reduced and prehensile, which allows carrying behaviour (Guinot *et al.* 1995). The sternal plate is very wide, especially at the level of somite 5, all sutures are interrupted, the sterno-abdominal cavity is rather deep, and the abdomen does not reach suture 4/5. The first two pleomeres are dorsal and clasped between the P4-P5 coxae. A typical press-button is present (Guinot 1979a, fig. 28), but strangely the prominence appears in a concavity of the sternal suture 5/6 (Figs 15C, D, 16A, B). In the numerous genera attributed to the subfamily (Holthuis & Manning 1990, figs 21h, i, 37c, 41b, c, 43h, i, 45h, i, 50h, i, 55i, 56i-k), it

looks as if in both sexes, this suture is sufficiently curved backwards to include the nodules, which face the sockets in the postero-lateral angles of abdominal segment 6. The extremely acute prominences and the deep sockets provide an efficient locking mechanism. We consider the unique course of the sternal suture 5/6 as a synapomorphy of the subfamily Dorippinae (not in the Ethusinae, see below).

Guinot (1979a: 139, pl. 25, figs 8, 9) observed in *Medorippe lanata* (Linné, 1767) the persistence of acute buttons and defined sockets in post-pubertal and even ovigerous females, wondering whether the mechanism continues to be functional. In dorippine females (Fig. 16A) the sterno-abdominal cavity is peculiar. The abdomen, which partly remains in the prolongation of the carapace, does not lie in an excavation on the sternal plate but occupies a posterior location against the almost vertical sternites 7 and 8. In consequence, the components of the holding system (at the level where the pleomere 6 faces the curve of the sternal suture 5/6, a curve present in females as in the males) are not affected by the broadening of the different structures and the modifications which occur on the posterior region after the puberty moult in females. The vulvae lie very close to the locking prominences. Perhaps only the thickness of the egg mass and the long pleopodal setae prevent locking. In an ovigerous female of *Neodorippe* aff. *callida* (Fabricius, 1798), from Australia, a firm closing was found using efficient buttons and sockets. The reexamination of all the dorippine species and observations of live animals are needed.

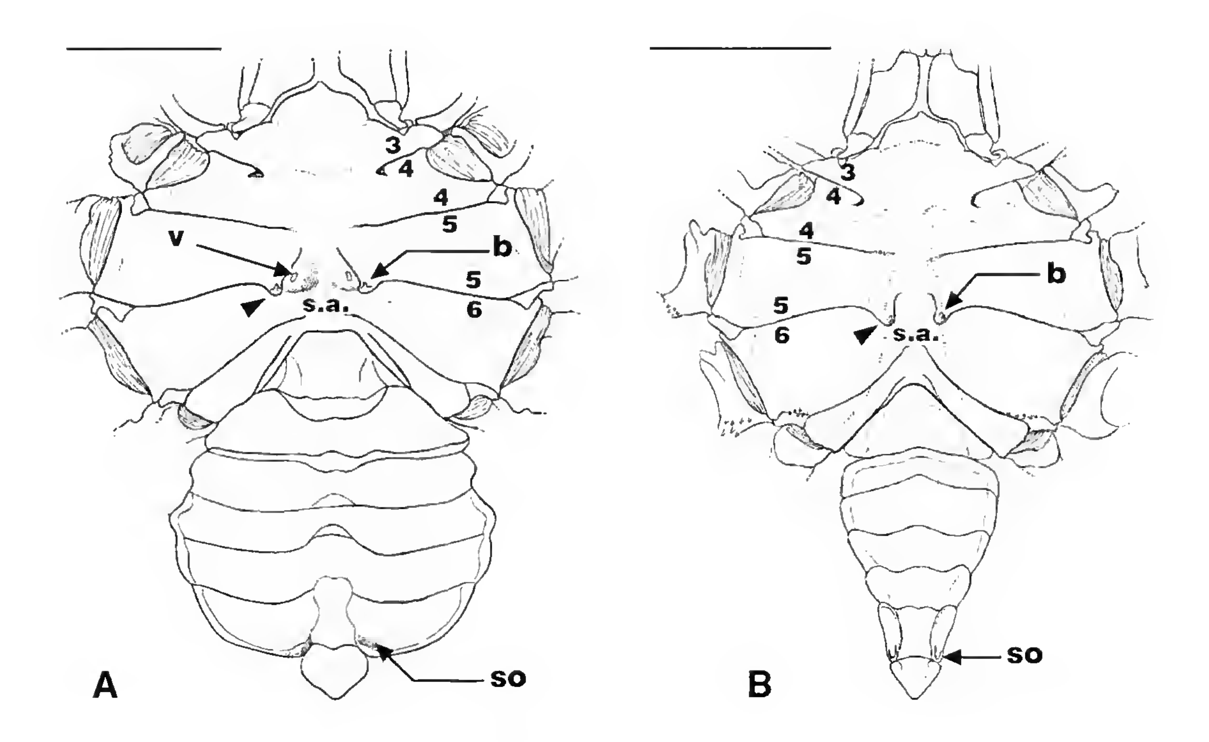


Fig. 16. — Locking apparatus in Dorippidae; *Medorippe lanata* (Linné), Dahomey (MNHN-B 20528); **A**, ♀ 22.6 × 30.5 mm; **B**, ♂ 19.1 × 23.3 mm, both with an effective apparatus. Abbreviations: **b**, button; **so**, socket; **s.a.**, sterno-abdominal cavity; **v**, vulva; **3/4**, **4/5**, **5/6**, sternal sutures 3/4, 4/5 and 5/6. Triangle shows the curve of the sternal suture 5/6 where the button is located. Setae were not figured. Scale bars: 1 cm.

SUBFAMILY ETHUSINAE Guinot, 1977

The ethusine subfamily differs in having the sternal suture 5/6 normally directed, without the curve seen in the dorippines. In *Ethusa* Roux, 1830 there is a strong prominence. In *Ethusina* Smith, 1884 males of all the species that were examined show a longitudinally elongated prominence, with a wide basis, resulting in a good locking with the large sockets. In mature females, with a cavity normally hollowed along the somites, both components of the apparatus are well-developed and permit effective locking.

Discussion

The distinct course of the sternal suture 5/6 with the locking prominence positioned inside a notch is an exclusive dorippine character, that allows a separation into the subfamilies Dorippinae and Ethusinae. In other respects, the persistence of the system in ovigerous females constitutes a synapomorphy of dorippids and ethusids, *i.e.* the family Dorippidae.

FAMILY RETROPLUMIDAE Gill, 1894

This small family, with two extant genera, was placed in the catometopous crabs despite the male gonopores opening on a tubercle at the base of P5 (Alcock 1899: 78, 79, Ptenoplacidae). The group, sometimes placed near the Palicidae (Balss 1957: 1662), was transferred to Dorippoidea with much reservation (Guinot 1978a: 151), then raised to suprafamilial level, without any connections with other brachyuran families (de Saint Laurent 1989). Several retroplumid fossils are known, which were assigned to Ocypodoidea (Glaessner 1960; Via Boada 1982) and/or in the Thoracotremata (Collins *et al.* 1994; Vega & Feldmann 1992).

Guinot (1979a: 148, fig. 30C, F), who observed only one female of a *Retropluma* species, indicated the peculiar locking apparatus of the family and emphasized that it was effective even in mature females. The fact that the retroplumid females retain a functional and very efficient mechanism, even in mature stages, was discussed (*ibid.*: 157). In the revision by de Saint Laurent (1989), who had at her disposal abundant material and established a new genus and several new species, a typical press-button was attributed to the retroplumids.

In both sexes the abdominal margins are coaptated with those of the sterno-abdominal cavity, the respective parts of each complementing each other. The external margin of pleomere 6 distally bears a characteristic lateral expansion, which is more or less pointed, and its edge immediately underneath is distinctly hollowed. Both abdominal parts (expansion + depression) perfectly fit into complementary parts (depressed and salient) at the margins of the sterno-abdominal cavity. A transverse ridge in the middle of sternite 5 ends in a thickened and sometimes granular prominence at the cavity's border. The lateral expansion of pleomere 6 fits into the depression in front of the prominence, which blocks the abdomen. This results in a strict adjustment and immobility of the abdomen, posterior to the telson.

In *Retropluma serenei* de Saint Laurent, 1989 there is a high and granular prominence, which is more developed in females than in males. In *Bathypluma spinifer* de Saint Laurent, 1989, in addition to the prominence, there is, near suture 4/5, a rounded nodule which is specially developed in females (Fig. 17C). The fact that this "button" is less marked in males (Fig. 17A, B) than in females, which are weakly dimorphic, is a unique adaptation among retroplumids.

The special structures shown by retroplumids deserve to be extensively studied. The fossil representatives of the family are similar to extant retroplumids. For example, the Upper Cretaceous *Costapluma concava* Collins *et* Morris (1975, pl. 97, figs 4, 8), the late Cretaceous *C. salamanca* Feldmann *et al.* (1997, fig. 3), and the Paleocene *C. nordestina* Feldmann *et* Martins-Neto (1995, fig. 3), which have their ventral surface preserved, show an abdomen embedded in a deep abdominal cavity which is excavated on the wide sternal plate, and a pleomere 6 with angles laterally expanded in a notch of sternite 4 near suture 4/5. It is obvious that the retention was efficient indeed.

FAMILY PALICIDAE Rathbun, 1898
(= CYMOPOLIIDAE Faxon, 1895)

The peculiar characters of the family, summarized by Guinot (1978a: 249; 1979a: 111, figs 30G, 31, pl. 19, fig. 5, pl. 24, fig. 9), indicated that, despite a male genital orifice opening in

a sternal position, it is an advanced heterotreme, with a coxo-sternal organization. When establishing two subfamilies, Palicinae Rathbun, 1898 and Crossotonotinae Moosa & Serène, 1981, and creating four new genera and six new species, Moosa & Serène (1981) did not elucidate their

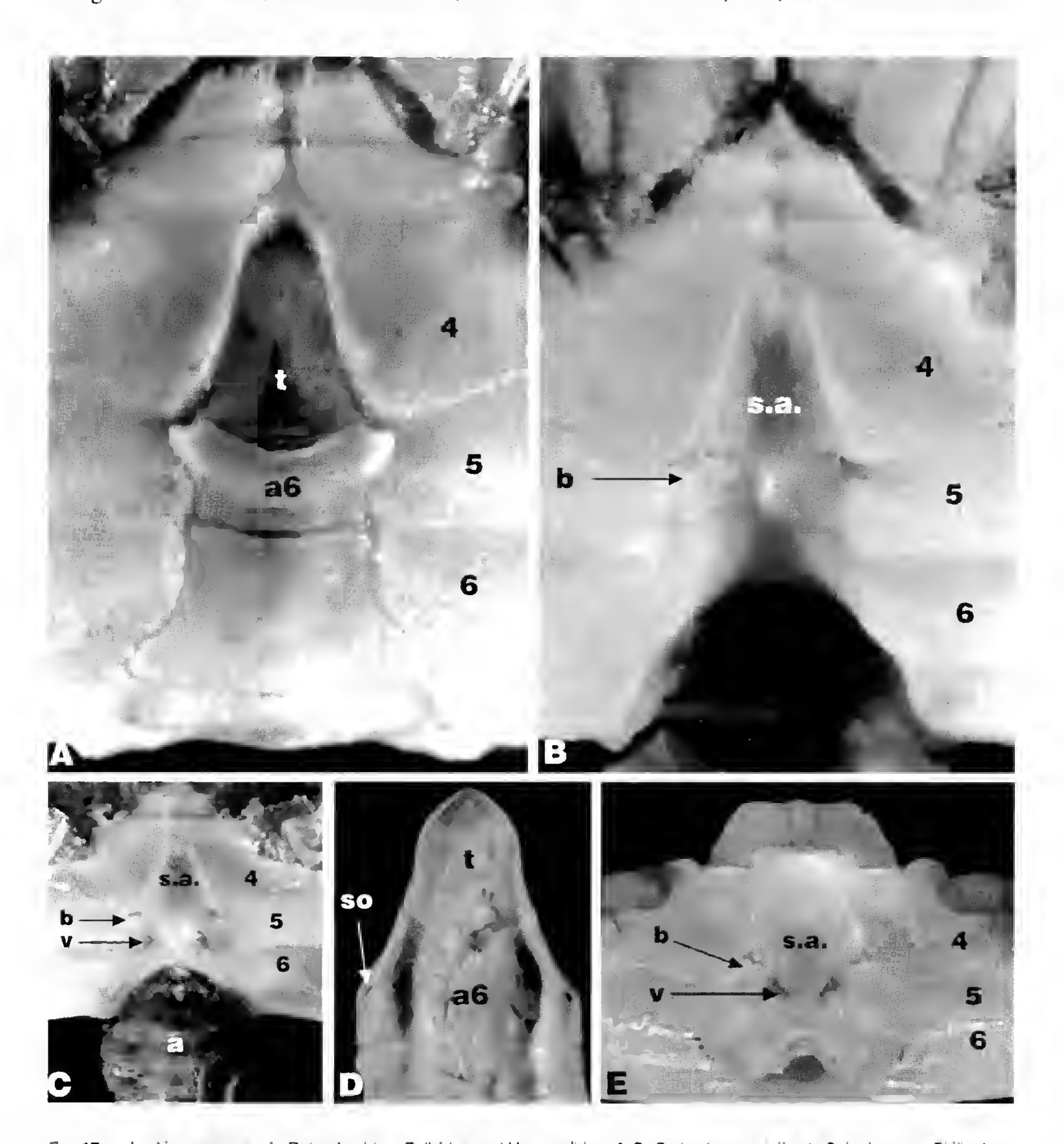


FIG. 17. — Locking apparatus in Retroplumidae, Palicidae and Hexapodidae: **A-C**, *Bathypluma spinifer* de Saint Laurent, Philippines (MNHN-B 7017): **A**, **B**, ♂ 12.4 × 15.6 mm: thoracic sternum with and without abdomen; **C** ♀ 11.9 × 14.9 mm: thoracic sternum without abdomen; **D**, *Palicus caronii* (P. Roux), ♂ 6 × 7 mm, Atlantic, "Le Talisman" (MNHN-B 16335): ventral surface of abdomen; **E**, *Hexapus sexpes* (Fabricius), ♀ 10.6 × 18 mm, Persian Gulf (MNHN-B 10209): thoracic sternum without abdomen: note the persistent buttons. Abbreviations: **a**, abdomen; **a6**, abdominal segment 6; **b**, button of the press-button; **so**, socket; **s.a.**, sterno-abdominal cavity; **t**, telson; **v**, vulva; **4**, **5**, **6**, sternites 4-6.

status. The phylogenetic relationships between palicids and dorippids remains questionable.
Nine palicine and crossotonotine species were examined. In the type species *Palicus caronii* (P. Roux, 1830) the sternite 5, located very anteriorly, bears a strong prominence just below the level of suture 4/5. The corresponding socket (Fig. 17D) is deeply hollowed along the external margin of pleomere 6, but in the whole anterior part of the segment instead of the usual posterolateral angle. The prominence remains as a non-functional corneous scar in ovigerous females.

FAMILY LEUCOSIIDAE Samouelle, 1819
Many leucosiids are typical heterotremes, having the male gonopore opening on the condylus of the P5 coxa, which is the plesiomorphic condition. Some advanced representatives, however, show sternal male gonopores (Guinot 1979a: 15, figs 45A-C, 55B-D; Guinot & Richer de Forges 1997: 478). (See Fig. 19C, male gonopore in a coxo-sternal position).
The sternal plate of leucosiids is rather wide and all the sutures are discontinuous. The well-defined episternites do not cover the condyli of P1-P4 in primitive genera such as *Iphiculus* Alcock, 1896 and *Pariphiculus* Adams *et* White, 1848, but in advanced forms such as *Leucosia* Weber, 1795 or *Philyra* Leach, 1817, the condyli of all pereiopods are covered. The sterno-abdominal cavity is very deep and often elongate as fat as the bases of Mxp3, and the anterior segments of the abdomen are gathered between the P5 coxae. The first abdominal segments, instead remaining dorsal as in many eubrachyurans crabs, are completely folded under the body, the first pleomere being covered by the posterior margin of carapace.
There are several ways to allow the pleon's base to be firmly grasped. These involve a connection between the sternal plate, pleomere 1 and the carapace; the transverse elongation of pleomere(s) 1 and/or 2; the development of a dorsally visible expansion of sternite 8, which surrounds the condylus of P5, and, additionally (as in *Philyra*), a depression inside the sterno-abdominal cavity at the surface of sternite 8, which receives the anterior part of pleomere 3. The pleopods themselves are coaptated with the bottom and margins of the sterno-abdominal cavity and with the abdomen (Fig. 19D). A perfect coaptation exists in *Leucosia* where, in addition, the G1 is situated in such a manner that it provides a place for the sternal locking structure.
Both male and female leucosiids are often found with the abdominal margins so closely fixed to the sternal plate that the abdomen is broken when lifted. Ovigerous females are known to have a brood chamber, sometimes closed like a box, because its margins are completely knitted to the edge of the sterno-abdominal cavity.
Guinot (1979a: 145-148) recognized two main types of abdominal retaining among leucosiids. In the two primitive genera *Iphiculus* and *Pariphiculus*, which have been recently re-examined, neither prominences nor sockets are present, and the highly movable telson sinks into the bottom of the cavity. In *Randallia* Stimpson, 1857 (Fig. 18) and *Ilia* Leach, 1817 (Fig. 19A) the sterno-abdominal cavity is very deep and markedly tapering, with its sides fitting the thick and sinuous edges of the abdomen. There is a mixture of coaptations by jux-

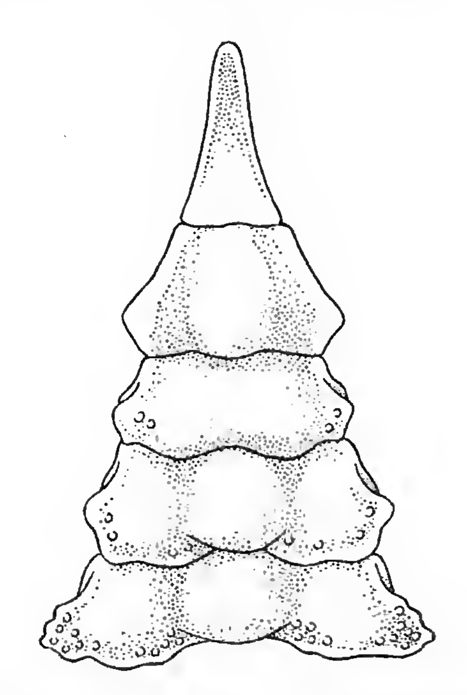


FIG. 18. — Abdomen in Leucosiidae (Phylirinae). *Randallia villosa* Chen, holotype, ♂: segments 3 through 6 plus telson. (After Chen 1989, fig. 11d).

taposition and by engagement, which characterizes the subfamilies Ebaliinae Stimpson, 1871, Cryptocneminae Stimpson, 1858, and part of the Philyrinae Rathbun, 1937.

In the subfamily Leucosiinae, *Leucosia* [the type species *L. craniolaris* (Linné, 1758) was not available] shows a particular configuration, with a sort of spur that projects inside the sterno-abdominal cavity, at the level of sternal suture 4/5. In *L. anatum* (Herbst, 1783) and *L. unidentata* de Haan, 1841 for example, the spur enters in a large notch excavated in the thick edge of the abdominal margin, and the abdomen becomes completely included in the smooth sternal surface (Fig. 19B-D). The endophragmal skeleton of *Leucosia* shows, at the level of endosternite 4/5, a pair of apophyses, that exactly corresponds to the pair of spurs (Fig. 19E). In addition to the spur of sternite 5, species of *Leucosia* show different developments of sternites 6 and 7 along the sterno-abdominal cavity, to which correspond complementary curves on the abdomen margins (Fig. 19B). The *Leucosia* species display a more or less acute spur on sternite 5.

A similar configuration is seen in the species examined of *Philyra* Leach, 1817, with various expansions of sternites 6 and 7. In *P. laevidorsalis* Miers, 1881, in which the spur of sternite 5 is not well developed, the sternite 6 protudes into a corresponding notch on the abdominal margin. In *P. pisum* de Haan, 1841 there are two granular protusions on sternites 5 and 6. In *Randallia villosa* Chen, 1989 the border of the sterno-abdominal cavity bears several protrusions with different notches in the edge of the abdomen, particularly a circular one at the junction of pleomeres 5 and 6 (Fig. 18). In all of its characters (carapace, pleopods) *R. villosa* obviously does not belong to the genus *Randallia*, a fact confirmed by the special configuration of the sterno-abdominal margin. A re-evaluation of all leucosiid members is needed.

Discussion

On the basis of *Leucosia ocellata* Bell, 1855, Bellwood (1996: 176, 191) indicated the absence of "cohesion nodules" in leucosiids and recorded these as absent in her matrix. It is clear, on the one hand, that in *Leucosia* the abdomen is not locked by a typical press-button, which supports the special category established by Guinot (1979a: 146) for the leucosiine spur. On the other hand, despite the presence of a hollow that, like the usual socket, (partly) belongs to pleomere 6, there is no true socket but only a notch at the junction of pleomeres 5 and 6. Endophragmal invaginations similar to the apophyses of the endosternite 4/5 observed in *Leucosia* were never found in relation to the buttons of the typical press-button.

Few brachyuran crabs exhibit, as in leucosiids, such a uniquely attached abdomen, joined with the rest of the sternal plate in such a way that the abdomen is broken when one attempts to lift it (Fig. 19B). Pinnotherids also show stages in which the abdomen is fused with adjacent zones of thoracic sternites (see below).

Both the sternal spur and abdominal notch are visible externally at the junction between the long pleomere 6 and the preceding segment. A characteristic of the locking mechanism in *Leucosia* is that the sternal part involved can be visible externally, in contrast to the typical press-button where the sternal part is covered by the folded abdomen and normally not seen. Such a structure may be easily recognized in fossils for the identification of *Leucosia* and allied genera. For example, the well preserved Neogene leucosiids studied by Morris & Collins (1991, figs 17b, 18, 24b) show the presence of a spur in a *Leucosia* species, and its absence in two *Iphiculus* species.

FAMILY PINNOTHERIDAE de Haan, 1833

The sternal plate is more or less wide, with all sutures discontinuous, and the sterno-abdominal cavity is deeply hollowed. The male sexual orifice of pea crabs, which opens on the sternum, has generally led to their assignment to the catometopous crabs. Rice (1980: 315) regarded the Pinnotheridae (with the Leucosiidae) as "the most advanced catometopous families". But this male configuration was reconsidered as coxo-sternal and, consequently, the family Pinnotheridae was transfered to the Heterotremata, instead of Thoracotremata (Guinot & Richer de Forges 1997).

It is difficult to determine the morphological characteristics of the apparatus in pinnotherids

because of the rareness of males and the weakness, loss or absence of specialized structures in soft individuals. In hard-shelled individuals belonging to *Ostracotheres tridacnae* (Rüppell, 1830) and *Pinnotheres pisum* (Linné, 1758), a double locking mechanism has been observed: a

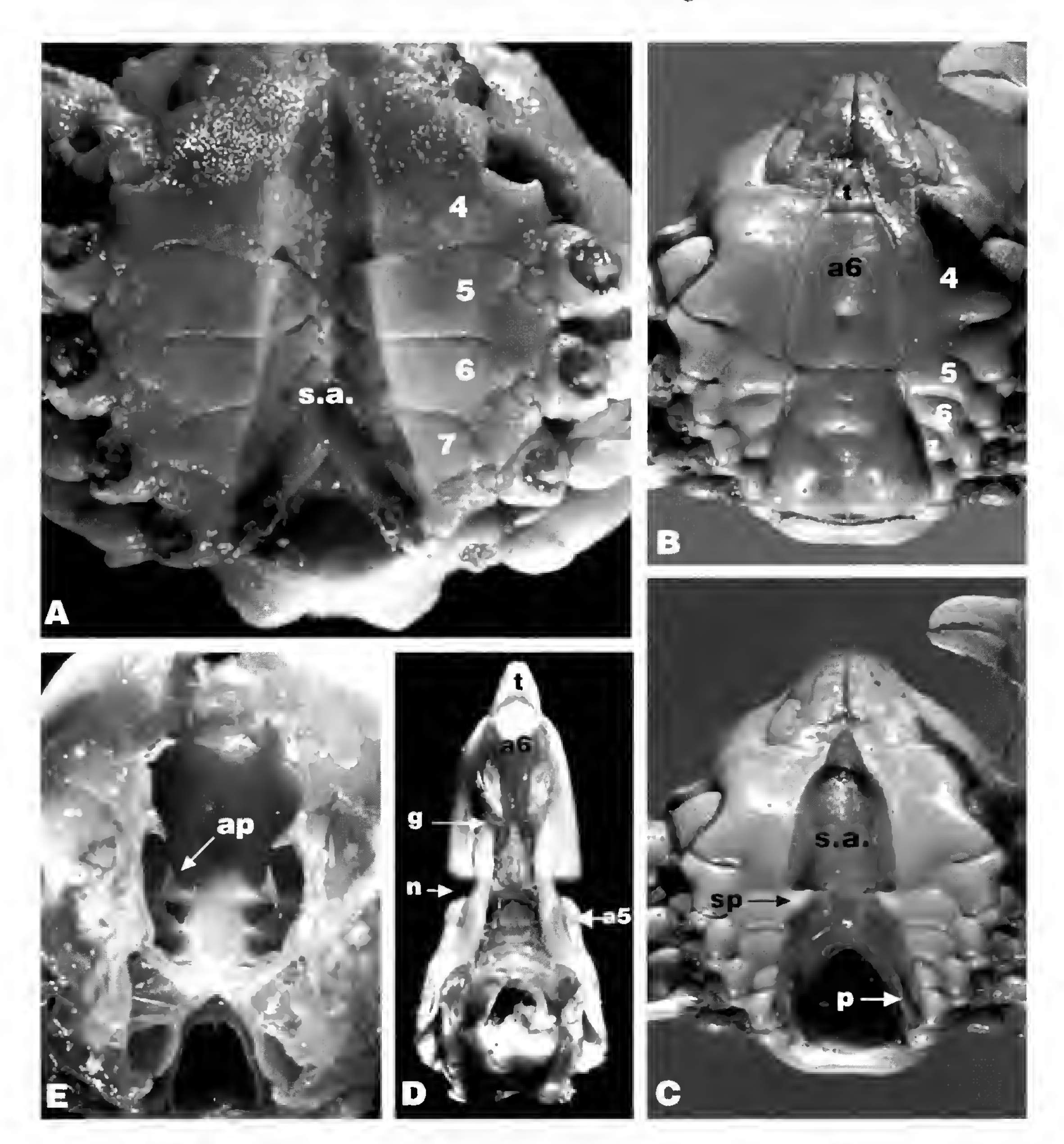


Fig. 19. — Leucosiidae (**A**. Ebaliinae; **B**-**E**, Leucosiinae), without a typical abdominal locking apparatus; **A**, *Ilia nucleus* (Linné), ♂ 27 × 26 mm, Mytilene, Port Vera (MNHN-B 19975); **B**, **C**, *Leucosia* sp. (identified as *L. unidentata* de Haan), ♂ 29 × 27 mm, in the vicinity of Tokyo (MNHN-B 16965): thoracic sternum with and without abdomen; **D**: ventral surface of abdomen; **E**, *Leucosia* sp. (identified *L. longifrons* de Haan), ♂ 21 × 20 mm, New Caledonia (MNHN-B 17525): endophragmal skeleton, with the pair of endosternal apophyses. Abbreviations: **a5**, **a6**, abdominal segments 5, 6; **ap**, endosternal apophysis; **g**, G1; **n**, notch; **p**, penis (male gonopore in a coxo-sternal position); **s.a.**, sterno-abdominal cavity; **sp**, spur; **t**, telson; **4**, **5**, **6**, **7**, sternites 4-7.

large knob on sternite 5 and a smaller one on sternite 6 (Guinot 1979a: 148, fig. 24D, pl. 24, figs 7, 8). Only one prominence on the lone sternite 5 was seen in *Pinnixa transversalis* (H. Milne Edwards *et* Lucas, 1843). In *Pinnotheres pisum*, Atkins (1926: 476, figs 1, 2) indicated one pair of prominences and sockets in a hard male stage, and also in young females which are almost indistinguishable from males.

Stauber (1945: 274, 277, 278, 280, figs 15, 16) studied living individuals of *Zaops ostreum* (Say, 1817) (as *Pinnotheres ostreum*, cf. Manning 1993a: 528; 1993b: 127), which is symbiotic with the oyster *Crassostrea virginica* (Gmelin), and recognized several distinct stages between the invasive crab stage and the adult. In a hard male stage (mean cw 2.13 mm) two pairs of knobs were present on thoracomeres 5 and 6 (shallower and smaller on the sixth) to which corresponded two pairs of shelf-like projections on pleomeres 6 and 5, "making a close-fitting efficient locking mechanism". In the first female stage (mean cw 1.83 mm), which invades the oyster, only the sets on thoracomere 5 and on pleomere 6 were present. During these masculine and feminine stages, it was impossible to lift the abdomen without injuring it. The same set occurred in the second female stage, but the mechanism was weakened by the thinner exoskeleton. For that stage and for the subsequent feminine stages (the last being the mature female), which had a very wide abdomen and no knobs, Stauber concluded that it was an adaptation to living within the mantle cavity of the host. In a masculine second stage (cw 2-4.8 mm), with a soft body, two pairs of sternal knobs and only one pair of abdominal structures on pleomere 6 were present, so that the abdomen was easily lifted from the sternum even in living crabs (*ibid.*: 280). Christensen & McDermott (1958), who re-investigated the biology of *Zaops ostreum* with new information and new terminology, and Christensen (1959) for *Pinnotheres pisum*, did not mention the presence or role of locking structures.

It is obvious that the locking system of pinnotherids varies during their life history. There is no information available to determine whether the remaining pinnotherid genera follow the same pattern as *Zaops ostreum*.

The prominence and socket (Fig. 26A, B) of a hard male of *P. pisum* were observed with the scanning electron microscope.

Family Calappidae de Haan, 1833

The sternal plate is relatively narrow but sutures 4/5 and 5/6 are discontinuous, being separated by a very small gap; the well-defined epsiternites cover condyli of P2-P4. The abdomen is rather long and lodged in a well-excavated cavity. There is a typical press-button, with prominences (appearing granulous under the binocular) close to sternal suture 4/5 (Guinot 1979a, pl. 14, figs 1, 2). Bellwood (1996: 176, fig. 2A) indicated some nodules located immediately behind the sternal suture 4/5 in the calappids that were examined.

Family Matutidae Macleay, 1838

The thoracic sternum is slightly enlarged, only the suture 4/5 is discontinuous and the sterno-abdominal cavity occupies a very small part of sternite 4. There is a typical press-button, with prominences not very far from the sternal suture 5/6 (Guinot 1979a, pl. 14, figs 4, 5). Bellwood (1996: 176, fig. 2C) indicated that the nodules were immediately located above the sternal suture 5/6 in the Matutidae that were examined.

Families Aethridae Dana, 1852 *emend.* and Hepatidae Stimpson, 1871

Guinot (1966-1967) rehabilitated the ancient Hepatinae Stimpson, 1871 (see also Ortmann 1892: 556, 569). The genus *Hepatus* Latreille, 1802, generally placed near *Calappa* Weber, 1795 and *Matuta* Weber, 1795 (Rathbun 1937: 234; Balss 1957: 1611-1612), was separated. The provisional designation Parthenoxystomata was used by Guinot to include, in addition to *Hepatus*, some allied genera that were previously classified in various high level taxa: *Aethra* Leach, 1816, attributed to the Parthenopidae (Rathbun 1925: 550; Balss 1957: 1629-1630; Garth 1958: 434, 467); *Osachila* Stimpson, 1871, included in Calappinae (T. Sakai 1965: 57) or in Matutinae (Rathbun 1937: 234; Balss 1957: 1612) or in Aethrinae *emend.* (T. Sakai 1976: 288; Huang 1989: 347); *Hepatella* Smith, 1869, and *Actaeomorpha* Miers, 1878 (see Guinot 1978b), tradi-

tionally attributed to the Leucosiidae Ebaliinae. The phylogenetic relationship of all these genera was supported by a morphocline. The genus *Sakaila* Manning *et* Holthuis, 1981 was subsequently included in the parthenoxystomatous group.

The affinities of these genera with the other calappids, represented by *Calappa*, and the parthenopids *sensu lato* remained questionable (that was the reason of the informal designation Parthenoxystomata), but the problem was often ignored and never solved. The familial designation Aethridae, generally not accepted, was used by Ng & Rodriguez (1986) who recognized four families in the large parthenopid group *sensu lato*: Daldorfiidae, Dairidae (see below), Parthenopidae *s.s.*, and Aethridae.

Bellwood (1996: 185, 186) confirmed the separate status of *Hepatus* with a familial rank, Hepatidae *pro parte* sensu Guinot, close to the Calappidae, and considered the two families Hepatidae and Calappidae as sister groups in the superfamily Calappoidea. The crucial question of the status of the parthenoxystomatous genus *Aethra* was omitted from the cladistic analysis of Bellwood. If further researches demonstrate that *Hepatus* and *Aethra* belong to the same clade, the family name Aethridae Dana, 1852 has priority over Hepatidae Stimpson 1871. *Osachila* contains several species, some of which have a more aethrid facies, while others look more like hepatids (Guinot 1966-1967: 836, 838).

In aethrids/hepatids the sternal plate is wider than in calappids, and, in contrast to calappids, the well-defined epsiternites do not cover the condyli of P2-P4. The sutures 4/5 and 5/6 are medially separated.

In males of *Hepatus* the external margin of every abdominal segment is sinuous and fits into a corresponding surface at the border of the very deep sterno-abdominal cavity. Sternite 5 also bears, posterior to a depression, a prominence which hangs on a well-delimited socket on the internal surface of pleomere 6. This is a case where the combination of a press-button apparatus and of multiple sternum/abdomen attachments allows a powerful holding of the pleon. Bellwood (1996: 176, fig. 2B) defined the organization in hepatids, attributing to sternal structures a location half-way between the two sutures 4/5 and 5/6 in hepatids, at least in the material that was examined. We have found that in *Aethra scruposa* (Linné, 1764), the type species of the genus, the nodule is more posterior and that, in some *Osachila* species, the wide prominence can be located close to suture 5/6.

In aethrid/hepatid females each sternite 6 and 7 bears a strong protuberance that fits into a notch on abdominal margin. After the moult of puberty a vestige of the socket can remain on the internal surface of pleomere 6.

The males of *Aethra* Leach, *Osachila* Stimpson and *Sakaila* Manning *et* Holthuis present a remarkable indentation on the particularly thick edge of the abdomen, to which complementary sinuous surfaces of the sterno-abdominal cavity correspond. The sculptured and eroded ornamentation of these regions provides a strong attachment. A sternal press-button is present. A socket is deeply excavated and defined by a strong superior margin. In females, protuberances on sternites (particularly at the base of the cavity) fit into the corresponding edge of the abdomen, which allows a perfect closing.

FAMILIES PARTHENOPIDAE Macleay, 1838 AND DALDORFIIDAE Ng *et* Rodriguez, 1986

The families Parthenopidae and Daldorfiidae are dealt with separately, awaiting a review of their phylogenetic relationships and precise status.

The margins of both sterno-abdominal cavity and abdomen display remarkable corresponding surfaces, with a deeply eroded complementary ornamentation, in contrast to the smooth cavity. The press-button is typical (Guinot 1979a: 138, pl. 17, figs 1-4).

FAMILY DAIRIDAE Ng *et* Rodriguez, 1986

Guinot (1967) showed the close relationship between *Daira* de Haan, 1833 (previously regarded as a xanthid) and *Dairoides* Stebbing, 1920. A family was established by Ng & Rodriguez (1986: 90, 97) for these genera, specialized but with plesiomorphic structures (notably G2 with a long and whiplike flagellum). The exact relationship with other parthenopids *sensu lato* needs to be established.

Daira and *Dairodes* have a similar locking apparatus. In *Dairoides kusei* (T. Sakai, 1938) a perfect coaptation was found in a male (cw 59 mm) but, in a larger male (55 × 71 mm), the two prominences did not fit into sockets since they were external to the abdomen (Guinot 1979a: 138, fig. 27A, pl. 17, fig. 9).

SUPERFAMILY MAJOIDEA Samouelle, 1819 (several families)

In the Majoidea, which contains about 800 species assigned to more than 150 genera and in which 50 suprageneric categories were listed (Manning & Holthuis 1981: 253), Garth (1958) and Griffin & Tranter (1986) recognized seven subfamilial taxa. In these two publications, five subfamilies received the same name: Majinae Samouelle, 1819, Inachinae Macleay, 1838, Mithracinae Macleay, 1838, Pisinae Dana, 1851, Oregoniinae Garth, 1958, whereas two had different names: Epialtinae Macleay, 1838 (*in* Griffin & Tranter = Acanthonychinae Stimpson, 1871, *in* Garth) and Tychinae Dana, 1851 (*in* Griffin & Tranter = Ophthalmiinae Balss, 1929, *in* Garth). On the basis of larval characters six majid subfamilies were considered by Ingle (1976): Oregoniinae, Acanthonychinae, Inachinae, Pisinae, Majinae, Ophthalmiinae. Guinot (1978) suggested that the majids may be raised to superfamily status, and Clark & Webber (1991) proposed a new classification of the Majoidea, distinguishing four major families: Majidae, Inachidae, Oregoniidae, and Macrocheiridae Dana, 1851. We proposed to consider a supplementary category, the Inachoididae Dana, 1851 (Drach & Guinot 1982, 1983; Guinot 1984; Guinot & Richer de Forges 1997).

It is beyond the scope of this paper to investigate the locking systems in such a large group. It appears that the majoid mechanism is a typical press-button. In certain majoid representatives, for example in most Inachinae [Fig. 20A, B: *Inachus dorsettensis* (Pennant, 1777)] and all Inachoidinae [Fig. 20C, D: *Pyromaia tuberculata* (Lockington, 1877); Fig. 20E, F: *Collodes leptocheles* Rathbun, 1894] the abdominal segment 6 is fused to telson in a pleotelson so that the sockets are unusually located on the last element of the abdomen. The button may be very acute, often positioned on oblique flanks of the sterno-abdominal cavity, and the socket extremely deep (see Figs 20B-D, F, 21A-F). In the majid genus *Thacanophrys* Griffin *et* Tranter, 1986 both button and socket may be persistent in adult females (Fig. 21E, F).

The family Hymenosomatidae Macleay, 1838 was recently affiliated with Majoidea by Guinot & Richer de Forges (1997), who provided information on the locking systems. Sternites 1-3 form a shield, more or less narrow and prolonged between the Mxp3; the plate constituted by sternites 4-7 is very wide, with all the sutures short, interrupted, and placed laterally. The undivided broad medial part of the plate corresponds to the absence of medial skeletal phragma. The sterno-abdominal cavity of males is generally very reduced in length, sometimes shallow, otherwise deep, in contrast to the large and often very specialized brood chambers found in females. The Hymenosomatidae differ from the usual brachyuran pattern of six abdominal segments plus telson in never having more than five pleomeres plus telson in both sexes. We regard the fusion of abdominal segment 6 with telson, that is the formation of a pleotelson, as an hymenosomatid synapomorphy. In the advanced species of the family, additional pleomeres may be fused to that terminal pleotelson, which leads to a weakly segmented abdomen, for example of only three elements (segments 3-5 fused to pleotelson) in the case of male and female *Crustaenia palawanensis* (Serène, 1971).

The configuration is of the press-button type, but with some specialized features. As for vulvae, the locking prominences are situated on the undivided part of sternal plate, often on the oblique flanks of the sterno-abdominal cavity; at first sight their belonging to sternite 5 is not obvious (Guinot 1979a: 110, 149, fig. 30A, pl. 20, fig. 8, pl. 23, fig. 6). Dissection of the skeleton permitted us to define the internal configuration of phragma and the exact place of the sternal prominences on somite 5 (Guinot & Richer de Forges 1997, figs 2A, C, E, 6F). In hymenosomatids the sockets appear laterally located at the pleotelson base but belong to pleomere 6 as in all Brachyura.

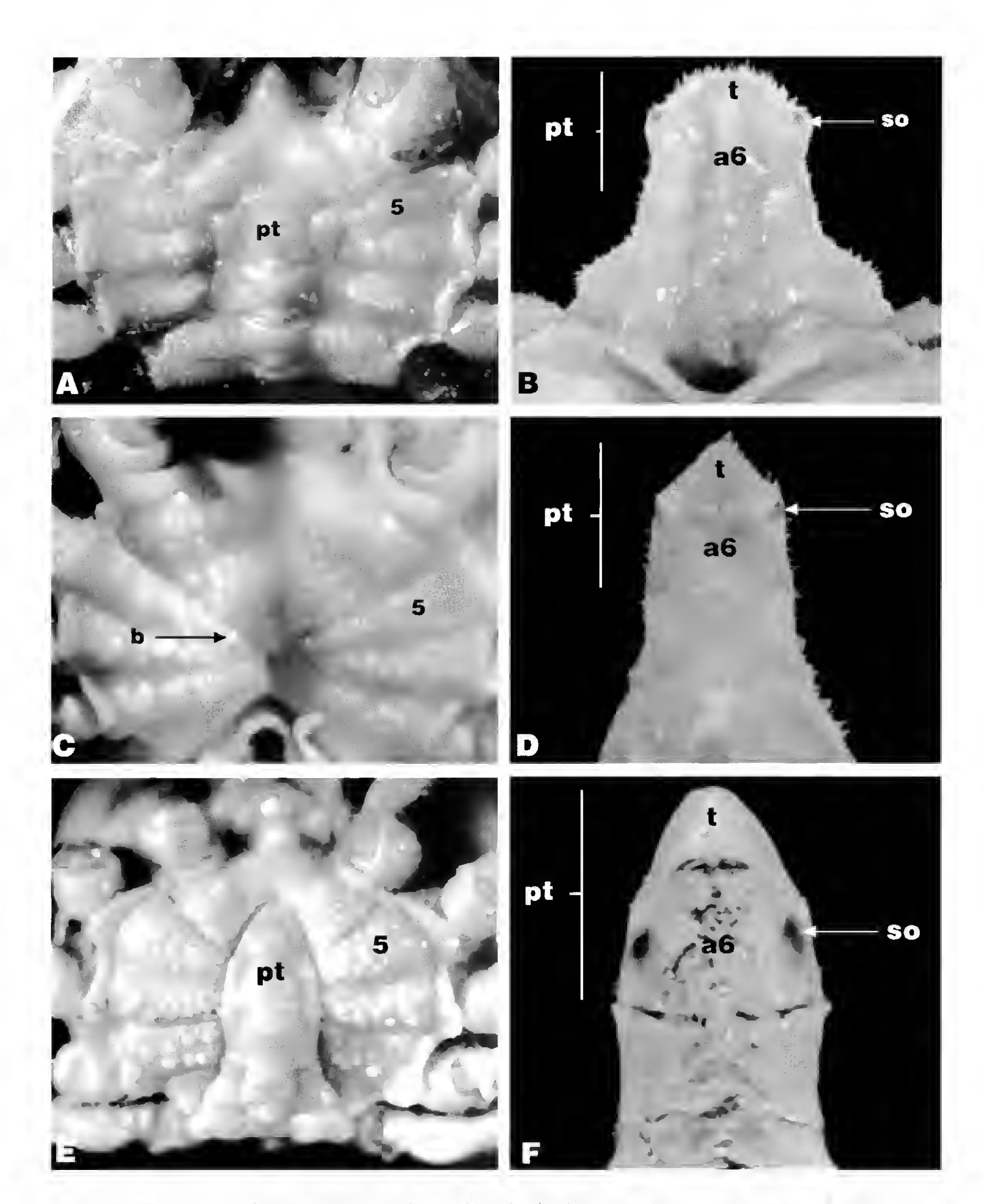


FIG. 20. — Locking apparatus in Majidae (**A**, **B**, Inachinae; **C-F**, Inachoidinae); **A**, **B**, *Inachus dorsettensis* (Pennant), ♂ 20 × 18 mm, Saint-Martin-de-Ré (MNHN-B 17337): **A**, thoracic sternum with abdomen; **B**, ventral surface of abdomen; **C**, **D**, *Pyromaia tuberculata* (Lockington), ♂ 17 × 12.2 mm, Lower California (MNHN-B 9290): **C**, thoracic sternum without abdomen; **D**, ventral surface of abdomen; **E**, **F**, *Collodes leptocheles* Rathbun, ♂ 17.5 × 13.2 mm, Gulf of Mexico (MNHN-B 14055): **E**, thoracic sternum with abdomen; **F**, ventral surface of abdomen. Abbreviations: **a6**, abdominal segment 6; **b**, button; **pt**, pleotelson; **so**, socket; **t**, telson; **5**, sternite 5.

Another characteristic feature of hymenosomatids is the presence of defined intercalated platelets, either completely articulated, movable as in *Odiomaris pilosus* (A. Milne Edwards, 1873) (Fig. 27) and *Amarinus angelicus* (Holthuis, 1968), or fused, the suture that delimits them being more or less discernible (Lucas 1980, fig. 7; Guinot & Richer de Forges 1997, figs 4A-E, 6B-E). We consider that the transformation series of the movable intercalated platelets into fused plates, then their complete integration to pleotelson, illustrate the stages towards the apomorphic condition. The intercalated platelets in the Hymenosomatidae correspond to the sockets in other brachyuran crabs and, as such, constitute the complementary abdominal parts for locking and are used for this purpose. When the delimited platelets have disappeared, only sockets remain excavated on the ventral surface of pleotelson's base (see Hypothesis about the homology uropod-socket).

Families Portunidae Rafinesque, 1815, Platyxanthidae Guinot, 1977, Eriphiidae Ortmann, 1893 (= Menippidae Ortmann, 1893), Carpiliidae Ortmann, 1893, Xanthidae Macleay, 1838, Panopeidae Ortmann, 1893, Bythograeidae Williams, 1980, Trapeziidae Miers, 1886, Pilumnidae Samouelle, 1819, Eumedonidae Miers, 1879, Geryonidae Colosi, 1923, Goneplacidae Macleay, 1838 *sensu lato* (not an exhaustive list)

There is a typical press-button. The button and the socket vary only according to their size, shape, microstructures (Bouchard, in preparation), and to their relative location on the surface of the corresponding somite, always on the surface of sternite 5 for the button and on the internal surface of pleomere 6 for the socket. See text and figures in Guinot 1979a.
The button and the socket (Fig. 26C, D) of the hydrothermal crab *Austinograea alayseae* Guinot, 1990 were observed with the scanning electron microscope.

Families of freshwater crabs (Deckeniidae Ortmann, 1897, Gecarcinucidae Rathbun, 1904, Parathelphusidae Colosi, 1920, Potamidae Ortmann, 1896, Potamonautidae Bott, 1970, Pseudothelphusidae Ortmann, 1893, Sundathelphusidae Bott, 1969, Trichodactylidae H. Milne Edwards, 1853)

All the representatives of these diverse brachyuran families are true freshwater crabs, without marine larval stages: they are restricted to freshwater habitats and, apparently, no members nor close relative are marine. They all have a male opening that is located on the P5 coxa: they belong in the Heterotremata. The existence of diverse forms of a penial groove, which is rudimentary in Pseudothelphusidae and partially covered by sternal parts in Trichodactylidae, could be considered as first stages in the process leading to coxo-sternal orifices (Rodriguez 1992; Ng & Rodriguez 1995).
It is usual that the abdomen retention is ensured by a typical press-button, but the configuration needs to be verified in all taxa.

Family Hexapodidae Miers, 1886

A doubtful and temporary assignment of the family Hexapodidae to the Thoracotremata was suggested by Guinot (1978a; 1979a: 114, 145, fig. 32). Hexapodids, that are highly modified (some species are known to live in tubes of annelids and on hydroids), appear to not belong to the catometopous group (*ibid.*: 215). The attribution of the family to the Heterotremata (Guinot & Richer de Forges 1997: 496, table 1) is in accordance with the ontogenetic data suggesting a close relationship to Goneplacidae (Pereyra Lago 1988). The apparatus belongs to the press-button type (Fig. 17E).

Family Cryptochiridae Paulson, 1875

The affinities of gall crabs with other brachyuran groups remain unclear, despite the essential findings of Kropp (1988, 1989, 1990) and Kropp & Manning (1985, 1987, 1996). The male orifice is indicated as opening in a sternal position, but possible states of this character need to be analysed. A coxo-sternal organization is admitted, leading to the inclusion of the family among the advanced Heterotremata (Guinot & Richer de Forges 1997: 496, table 1).

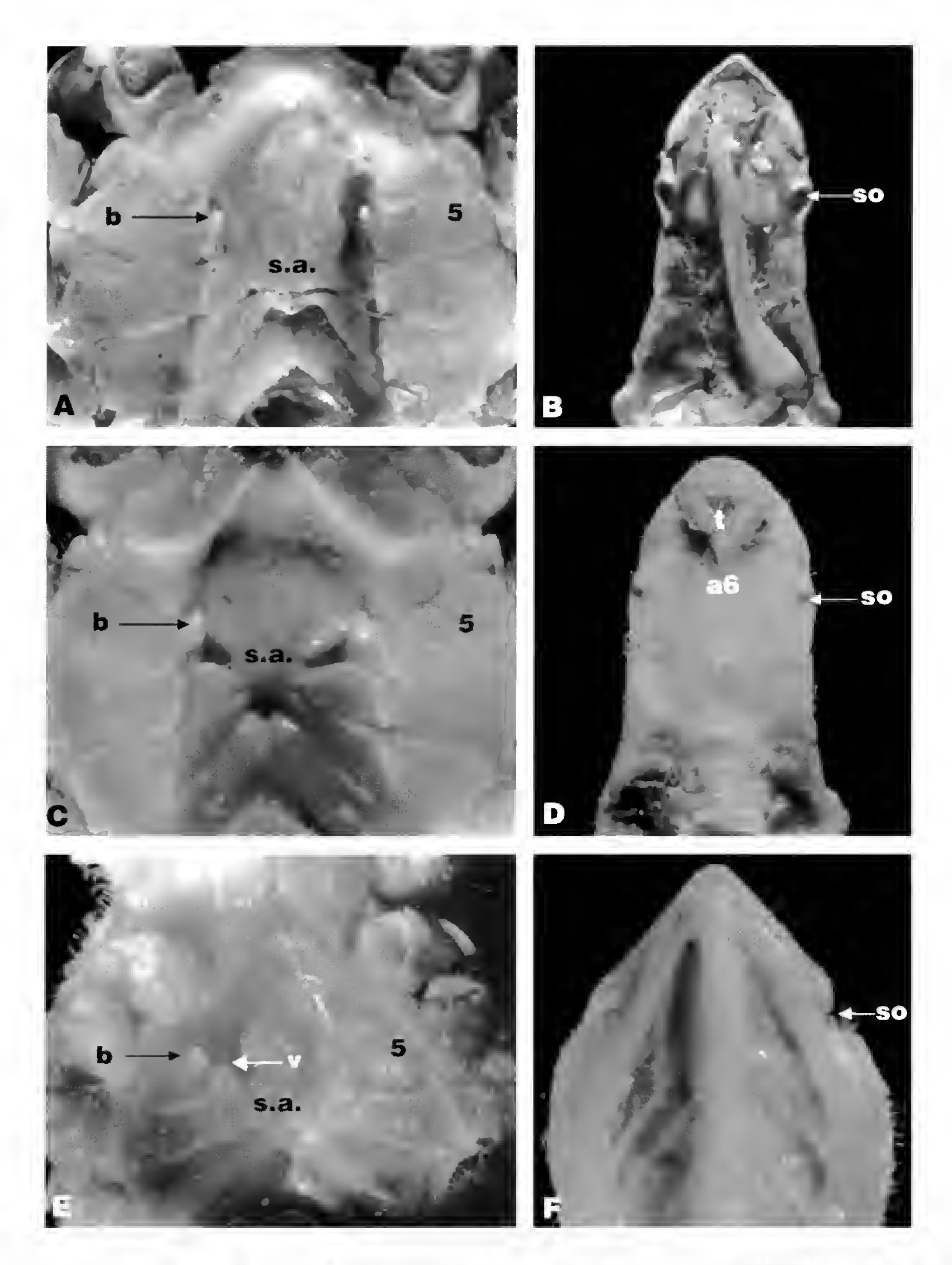


Fig. 21. — Locking apparatus in three majid species of *Thacanophrys* Griffin *et* Tranter; **A**, **B**, *Thacanophrys albanyensis* Ward (as *Chlorinoides barunai* Serène), ♂ 26 × 14 mm holotype, Indonesia (MNHN-B 17817); **A**, thoracic sternum without abdomen; **B**, ventral surface of abdomen; **C**, **D**, *Thacanophrys harmandi* (Bouvier) (as *Acanthophrys harmandi*), ♂ 46 × 24.5 mm, holotype, in the vicinity of Tokyo (MNHN-B 22330): **C**, thoracic sternum without abdomen **D**, ventral surface of abdomen; **E**, **F**, *Thacanophrys longispina* (de Haan) (as *Chorinus longispinus*), ♀ 23 × 27.4 mm, Japan (MNHN-B 17853): **E**, thoracic sternum without abdomen: note the persistent buttons; **F**, ventral surface of abdomen, with persistent sockets. Abbreviations: **a6**, abdominal segment 6; **b**, button; **s.a.**, sterno-abdominal cavity; **so**, socket; **t**, telson; **v**, vulva; **5**, sternite 5.

The extensive studies of Kropp reveal a wide range of configurations exhibited by the family, in particular with regard to the thoracic sternum, often illustrated in the females. The sternal plate varies from relatively narrow (*Cryptochirus* Heller, 1861) to wide or very wide (*Hapalocarcinus* Stimpson, 1859, *Pseudohapalocarcinus* Fize *et* Serène, 1956). The sternal sutures 4/5 and 5/6 are always interrupted, but in the posterior part of the plastron the sutures are diversely arranged. The sutures 6/7 and 7/8 remain continuous in: *Cryptochirus*, *Lithoscaptus* A. Milne Edwards, 1862 *pro parte*, *Zibrovia* Kropp *et* Manning, 1996, *Opecarcinus* Kropp *et* Manning, 1987 *pro parte*, *Fizesereneia* Takeda *et* Tamura, 1980. Only suture 7/8 may remain continuous, the 6/7 suture being more or less largely interrupted, in: *Lithoscaptus* pro parte, *Opecarcinus* pro parte, *Hiroia* Takeda *et* Tamura, 1980. The posterior sutures, 6/7 and 7/8, are interrupted, so that all the sutures are interrupted on the largely undivided, broad sternal plate, in: *Hapalocarcinus*, *Pseudohapalocarcinus*, *Fungicola* Serène, 1966, *Pseudocryptochirus* Hiro, 1938, *Xynomaia* Kropp, 1990 (not exhaustive lists).

The shape of the sterno-abdominal cavity and the precise location of the abdomen on the ventral plate are not well-kown in cryptochirids. The existence of a locking apparatus was never reported in males, always smaller than the females and relatively rare. The abdomen seems to be ventrally folded, without special morphological devices to hold it (R. K. Kropp pers. com.). It is noteworthy that absence of any apparent structures occurs in forms finding protection within galls or in open pits formed in corals.

THORACOTREMATA Guinot, 1977

The Thoracotremata, sternitreme for the female orifice (vulvae on sternite 6), show a constant sternal location of the male pores, which is on sternite 8 but in various places in relation to the sternal suture 7/8, so that the sternal male opening constitutes a multistate character (Guinot 1979a: 218, figs 53, 54, 55F-H, 56). The section Thoracotremata includes only littoral, amphibious and terrestrial brachyuran crabs (the genus *Planes* Bowdich, 1825 excepted) in marine or brackish habitats, with diverse representatives adapted to freshwater existence (Guinot & Richer de Forges 1997: 496, table 1).

In all representatives of the Thoracotremata the thoracic sternum is wide or very wide, the sutures 4/5 through 7/8 are interrupted, the generally deep sterno-abdominal cavity is often anteriorly delimited by a cristiform margin, the abdomen forms a thin plate, and the male orifice always opens on the sternum. A non-origination of the male gonopore and penis from P5 coxa, *i.e.* a direct sternal emergence, was observed in *Ocypode cursor* (Linné, 1758) in which the penis emerges near the end of thoracic suture 7/8 (Guinot 1979a, fig. 56). Regarding the gonopore/penis organization, the thoracotrematous character state appears either with a proximity to P5 coxa (Grapsinae, Plagusiinae, a part of Gecarcinidae and Sesarminae) or a location that is completely sternal, for example in the Ocypodidae. It is now obvious that the Thoracotremata *sensu* Guinot (1977, 1978, 1979) display various conformations of male ducts and openings: this emphasizes the necessity of additional information and further investigations (R. von Sternberg pers. com.).

Family Grapsidae Macleay, 1838

In both subfamilies Grapsinae and Plagusiinae there is a complete typical press-button apparatus, persistent and apparently functional throughout life. In the Plagusiinae the socket is located in the postero-lateral and external angles of abdominal segment 6, while in the Grapsinae the socket is similarly positioned in the postero-lateral part but generally far from the external margin of the abdomen. In both subfamilies Varuninae and Sesarminae, the locking mechanism is also of the press-button type: either it is present throughout life or tends to disappear in large crabs (even in males) or it is completely lost.

Subfamily Grapsinae Macleay, 1838

Within the genus *Grapsus* Lamarck, 1801, as in *G. grapsus* (Linné, 1758) and *G. tenuicrustatus* (Herbst, 1783) (Fig. 22A), there is an acute prominence, persistent in males throughout life (Hartnoll 1965: 128), and a socket far from the

external margin of the sterno-abdominal cavity (Guinot 1979a: 142, pl. 20, figs 1, 2). In *Goniopsis cruentata* (Latreille, 1803) the locking apparatus is functional only in immature females and in all males.

In *Pachygrapsus* Randall, 1839 the press-button was studied by Pérez (1933a, 1933b) and Vernet-Cornubert (1958). In male *P. transversus* (Gibbes, 1850) and *P. gracilis* (de Saussure, 1858) the mechanism is functional in all sizes, then throughout life, appearing in the first stages of post-larval existence and only regressing in mature females, which have a widened abdomen (Hartnoll 1965: 135, 136).

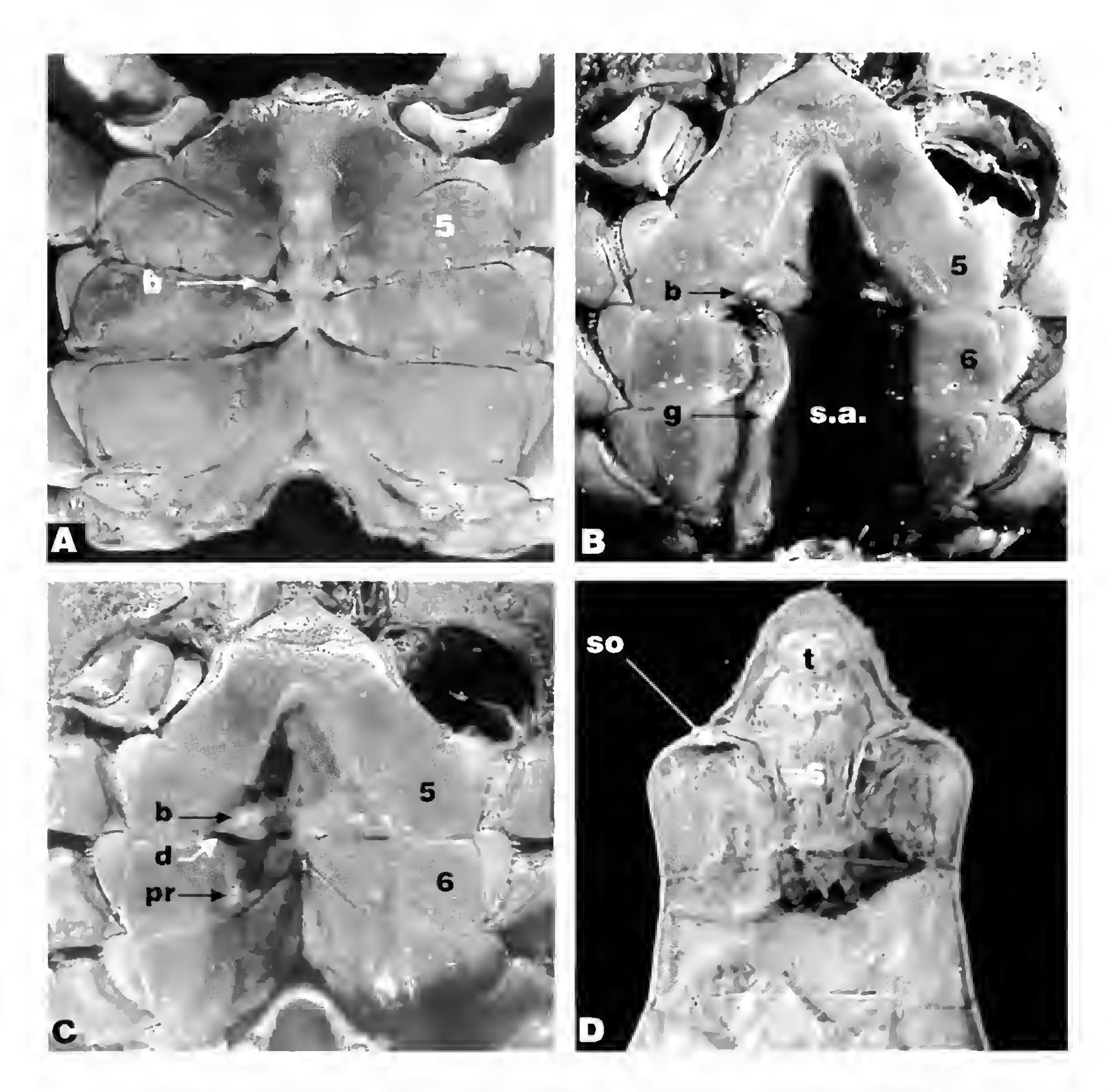


Fig. 22. — Locking apparatus in Grapsidae, subfamily Grapsinae; **A**, *Grapsus tenuicrustatus* (Herbst), ♂ 65 × 72 mm, Sainte-Luce (MNHN-B 11541); **B-D**, *Metopograpsus latifrons* (White), ♂ 28.8 × 32.8 mm, type series of *M. pictus* A. Milne Edwards, probably New Caledonia (MNHN-B 12882); **B** and **C**, thoracic sternum with and without G1; **D**, ventral surface of abdomen. Abbreviations: **a6**, abdominal segment 6; **b**, button; **d**, depression to receive the apex of G1; **g**, G1; **pr**, projection on sternite 6; **so**, socket; **s.a.**, sterno-abdominal cavity; **5**, **6**, sternites 5 and 6.

In the material of the genus *Geograpsus* Stimpson, 1858 that was examined, for example *G. lividus* (H. Milne Edwards, 1837), the press-button is typical, with the socket far from the external margin of the abdomen and sometimes horizonral.
In *Metopograpsus* H. Milne Edwards, 1853, as in *M. frontalis* Miers, 1880 and *M. oceanicus* (Jacquinot, 1853), the button is very prominent and the socket wide, without defined borders. The most striking case is shown by *M. latifrons* (White, 1847) (Fig. 22B-D: male of the type series of *M. pictus* A. Milne Edwards. 1867). The button on somite 5 is very elevated, transversely elongated, and offers an uneven surface. There is a close coaptation between the button and the male first gonopod: the T-shaped apex of G1 comes in contact with the posterior portion of the prominence and is situated in a corresponding depression hollowed on the surface of the sterno-abdominal cavity, just behind the button and at the level of suture 4/5. In addition, a rough prominence on somite 6 appears to limit sideways movement of the adjacent pleopod. In *Metopograpsus messor* (Forskäl, 1775) and *M. thukuhar* (Owen, 1839) the butron is smaller, rounded, not transversely elongated, and the apex of G1 is not T-shaped. It is doubtful, however, that all these species actually belong to the same genus.
In *Planes* Bowdich, 1825 the button is very close to the sternal suture 5/6 and the socket is near the external margin of the abdomen.

Subfamily Plagusiinae Dana, 1851
In all the examined species of *Plagusia* Latreille, 1804, *P. depressa* (Fabricius, 1775), *P. immaculata* Lamarck, 1818 and *P. glabra* Dana, 1851 (Fig. 23C-D), the sternal prominence is strong, looking more or less corneous. This corneous aspect is due to a scaly paving, observed with the scanning electron microscope (Fig. 26F, *P. immaculata*) (Bouchard in preparation). The deep socket persists and functions throughout life, except for post-puberty females where only a sternal scar remains visible (Guinot 1979a: 144, pl. 18, figs 9-11).
In *Percnon* Gistel, 1848, *P. planissimum* (Herbst, 1804), *P. affine* (H. Milne Edwards, 1853), *P. abbreviatum* (Dana, 1851), and *P. guinotae* Crosnier, 1965 were examined: the button has a wide base, forming a large prominence, and its surface looks corneous; the socket is deep and outlined with a strong thickening (Guinot 1979a, pl. 23, figs 2, 3).

Subfamily Varuninae H. Milne Edwards, 1853
The subfamily Varuninae, which includes more than fifteen genera living in estuarine and brackish or freshwater habitats, forms an artificial grouping that needs re-evaluation. It similarly appears heterogeneous in respect of the locking system.
In *Varuna litterata* (Fabricius, 1798) (*cf.* Guinot 1979a: 142, pl. 20, fig. 5) (Fig. 23A) and in the species of *Gaetice* Gistel, 1835, *Hemigrapsus* Dana, 1851, *Brachynotus* de Haan, 1833, *Pyxidognathus* A. Milne Edwards, 1878, and *Ptychognathus* Stimpson, 1858 that were examined, a typical press-button was present and persistent throughout the life in males, with a socket a little remote from the abdominal margin. In *Euchirograpsus* H. Milne Edwards, 1853, *E. americanus* A. Milne Edwards, 1853, *E. liguricus* H. Milne Edwards, 1853 and *E. timorensis* Türkay, 1975 that were examined had a specially acute button and a socket posteriorly defined by a strongly calcified border, which suggests that the genus is misplaced in the Varuninae.
A small button and a socket are present in *Eriocheir sinensis* H. Milne Edwards, 1854 (Fig. 23B), but the locking mechanism is no longer efficient in males beyond a carapace width of about 23 mm even if both morphological constituents are still present (Hoestlandt 1940: 21, fig. 8; 1948: 55). The zone bearing the acute button is covered by setae, and the socket seems the first to disappear, even when the button is not yet lost (Guinot 1979a: 142, pl. 23, fig. 1). In the male material of *E. japonica* (de Haan, 1835) that was examined, the button is small but remains present, in a notch left by the setae of G1, and the socket is weak. In specimens of *E. formosa* Chan, Hung *et* Yu, 1995 (a species to be referred to a new genus, *cf.* Guo *et al.* 1997) that were examined, the button is always small, the setae on G1 being in contact with the button; the diffuse socket seems to be ineffective.
In *Acmaeopleura* Stimpson, 1858 and *Tetragrapsus* Rathbun, 1918, the button is blunt and the soc-

ket weak. In *Cyrtograpsus* Dana, 1851, *C. angulatus* Dana, 1852 was examined: the large males were devoid of locking structures; a male measuring 14.6 × 17.4 mm bore a pair of minute buttons, covered by the G1 setae, but had obsolete sockets; in a smaller individual measuring 11.9 × 14 mm, however, the buttons were already lost.

Members of the genus *Orcovita* Ng *et* Tomasick, 1994, all anchialine or cavernicolous, possess an apparatus of the press-button type, with a marked button but only a diffuse socket (to be corrected in the diagnosis given by Ng, Guinot & Iliffe 1996), so that the abdomen seems to be not efficiently retained by this mechanism.

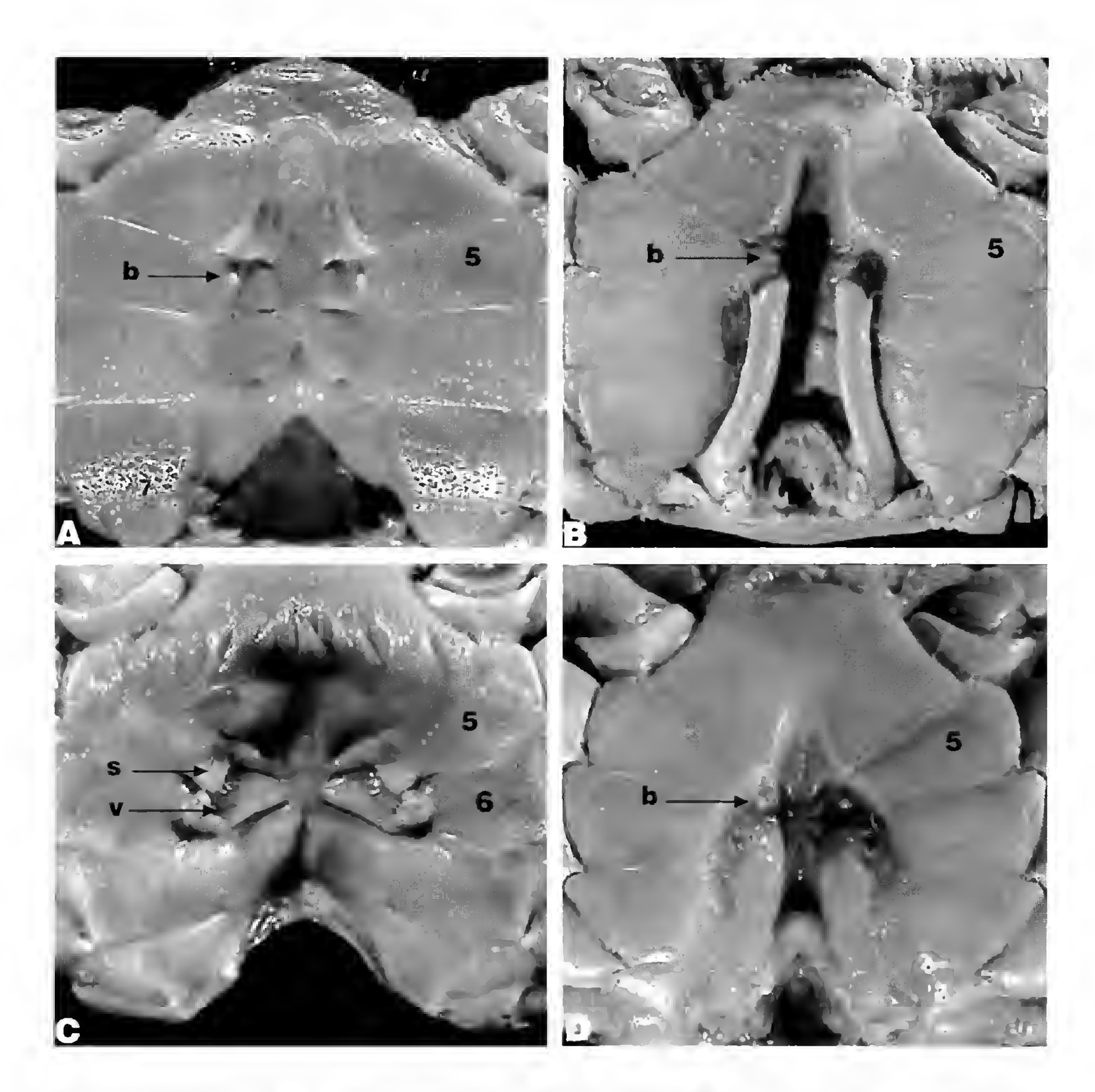


Fig. 23. — Locking apparatus in Grapsidae, subfamilies Varuninae and Plagusiinae; **A**, *Varuna litterata* (Fabricius), ♂ 29 × 31 mm, Madagascar (MNHN-B 16777); **B**, *Eriocheir sinensis* H. Milne Edwards, ♂ 71 × 75 mm, Escaut (MNHN-B 12581): button absent (setae were partly removed from right G1); **C**, **D**, *Plagusia glabra* Dana, near Sydney (MNHN-B 11700): **C**, ovigerous ♀ 35 × 38 mm: button persistent as a scar; **D**, ♂ 32 × 33.5 mm. Abbreviations: **b**, button; **s**, scar of the button; **v**, vulva; **5**, **6**, sternites 5, 6.

SUBFAMILY SESARMINAE Dana, 1851

The subfamily Sesarminae, an artificial grouping, is among the largest brachyuran subfamilies, with representatives that are intertidal, often mangrove dwellers, or adapted to freshwater, or very terrestrial (Ng 1988). In the sesarmine species that were examined the button was small and generally did not work after a certain size (sometimes at a size well below that of puberty), or was obsolete or absent; if present, the socket was weak.

In *Sesarma* Say, 1817 (type species *S. reticulatum* Say, 1817) and in allied genera the configuration is not constant. The sternite 5, often covered by setae, may be covered by G1. In the male material that was examined the small-sized individuals had a very small button, which could disappear at a particular molt, and a socket which was imperceptible under the binocular.

In *Sesarma* (*Chiromantes*) *bouzardi* (Desmarest, 1825) the locking mechanism seems to be functional. A well-developed prominence was observed on sternite 5 as well as a small socket in the postero-lateral corner of pleomere 6. This apparatus remains apparently constant and functional at any (molting stage) size of the individuals. In *S.* (*Perisesarma*) *alberti* Rathbun, 1921 a small sternal prominence is observable at any growing stage of the individuals despite the socket not being well-differentiated.

In *Sesarma (Chiromantes) guttatum* A. Milne Edwards, 1869 the button disappears beyond the size 12.9 × 16.2 mm. In *S. (Holometopus) ricordi* H. Milne Edwards, 1853, small individuals (cl less than 7 mm) show a normal locking apparatus, but this becomes non-functional in larger males: only vestigial tubercles remain on the sternum and they become smaller with increasing body size (Hartnoll 1965: 133). Young individuals of *Neoepisesarma* (*Neoepisesarma*) *mederi* (H. Milne Edwards, 1853) have a minute button near sternal suture 4/5 and a small socket, but these structures tend to disappear at large sizes. In *Neosarmatium meinerti* (de Man, 1887) the button is present in a male measuring 31 × 37 mm but is lost in a male measuring 36.5 × 42.7 mm. In *Sarmatium* Dana, 1851 the button is small or absent, and there is no socket.

In other sesarmine species the absence of buttons even before the moult of puberty in males is possible. In living *Sesarma* (*Sesarma*) *curacaoense* de Man, 1892, Hartnoll (1965: 139) noticed the absence of any abdominal locking apparatus. *S.* (*Sesarma*) *reticulatum*, *S.* (*Chiromantes*) *haematocheir* (de Haan, 1833), *S.* (*Chiromantes*) *dehaani* H. Milne Edwards, 1853, *S.* (*Chiromantes*) *guttatum* A. Milne Edwards, 1869, *S.* (*Geosesarma*) *maculatum* de Man, 1892, *Parasesarma plicatum* (Latreille, 1803) perhaps also, but an examination of specimens of all sizes is necessary. No button was observed in *Neosarmatium smithi* (H. Milne Edwards, 1853), *N. meinerti* (de Man, 1887), and *N. trispinosum* Davie, 1994.

In the examined species of the genera *Helice* de Haan, 1835 and *Pseudohelice* K. Sakai, Türkay *et* Yang, 1996, only a very minute tubercle exists on sternite 5 in males. It does not correspond to any (perceptible) socket, and locking does not appear possible. In *H. crassa* Dana, 1851 and *Pseudohelice leachii* (Hess, 1865) the tubercle disappears beyond a certain size in males. In all the examined male individuals of *H. tridens* de Haan, 1835 a second minute granule is present on the posterior portion of somite 5.

In *Cyclograpsus* H. Milne Edwards, 1837 the button is small or lost and the socket absent. The apparatus is vestigial in small individuals of *C. integer* H. Milne Edwards, 1837 (Hartnoll 1965). The sternite 5 is covered by the long male first gonopods in *C. punctatus* H. Milne Edwards, 1837, while in *C. integer* the gonopods are shorter and the sternite is free.

In *Metaplax* H. Milne Edwards, 1852 the button is absent or doubtful, and there is no apparent socket. In *Chasmagnathus* de Haan, 1833 the button is small and there is no discernible socket. In *Aratus pisonii* (H. Milne Edwards, 1837) no trace of button or socket was found, even in males. Observing living animals from Jamaica, Hartnoll (1965: 121, 145) recorded that the locking mechanism is completely lost in this tree climbing crab. It was remarked that in sesarmine species the disappearance of the apparatus is not accompanied by any overall change in the abdomen appearance, while in *Aratus* H. Milne Edwards, 1853, the male abdomen is large, somewhat resembling that of mature females. Hartnoll suggested that this "feminization" could perhaps account for the loss of the locking system.

FAMILY OCYPODIDAE Rafinesque, 1815

SUBFAMILY OCYPODINAE Rafinesque, 1815
We examined most species of the genus *Ocypode* Weber, 1795. The button is very small in *O. ceratophthalmus* (Pallas, 1772), *O. saratan* (Forskål, 1775), *O. cordimanus* Latreille, 1818, *O. platytarsis* H. Milne Edwards, 1852, *O. africana* de Man, 1881, *O. madagascariensis* Crosnier, 1965. It is absent in *O. cursor* (Linné, 1758) (Fig. 24B),

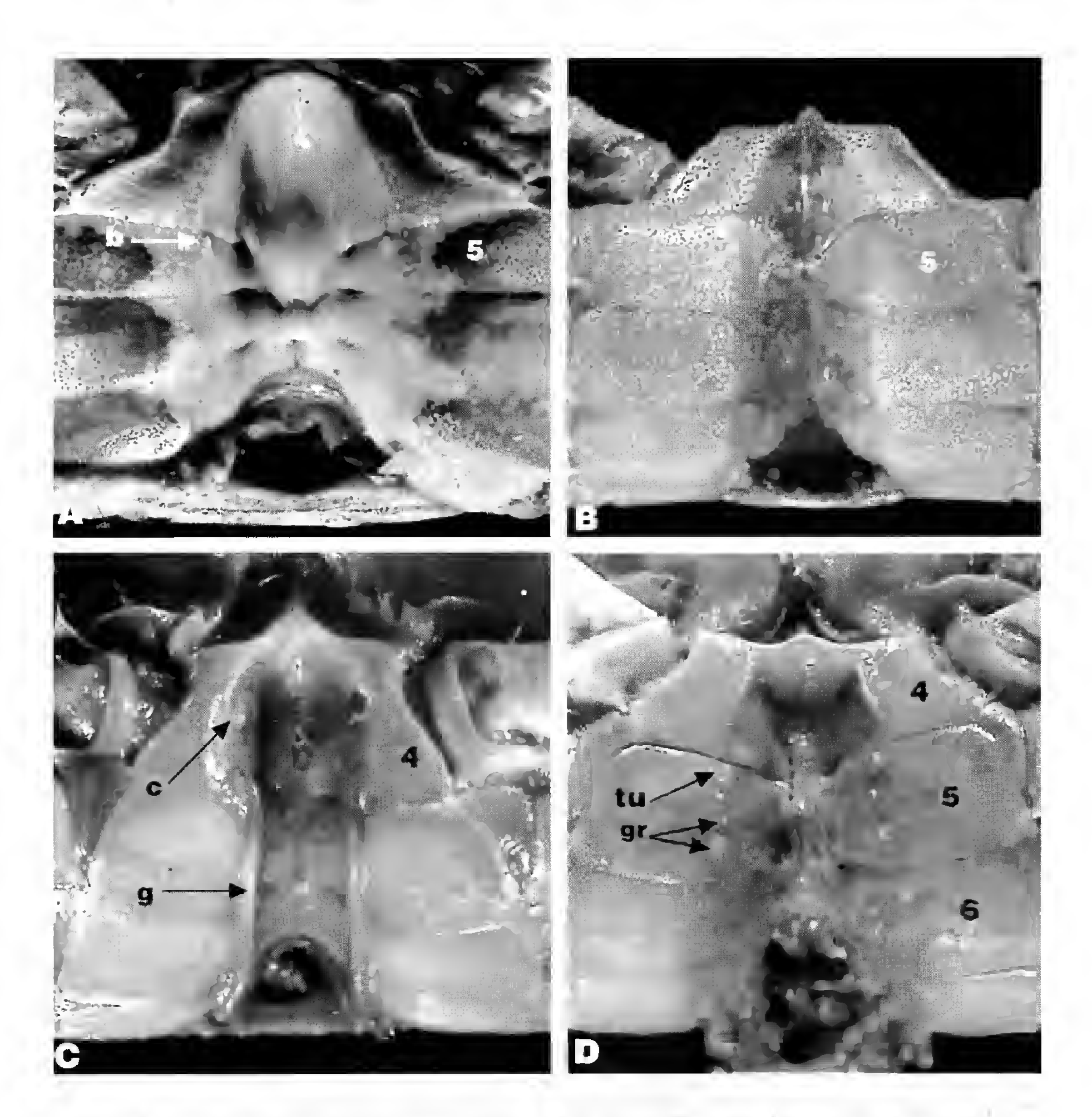


FIG. 24. — Locking apparatus in Ocypodidae, subfamilies Macrophthalminae and Ocypodinae; **A**, *Macrophthamus* (*Venitus*) *latreillei* (Desmarest), ♂ 38 × 51 mm, NW coast of Madagascar (MNHN-B 12614): button present; **B**, *Ocypode cursor* (Linné), ♂ 36 × 45 mm, Dakar (MNHN): button absent; **C**, *Uca* (*Boboruca*) *thayeri* Rathbun, ♂ 20 × 31 mm, French Guiana (MNHN-B 12049): two horizontal carinae on sternite 4; **D**, *Uca* (*Afruca*) *tangeri* (Eydoux), ♂ 26 × 39 mm, Dakar (MNHN-B 12027): a marked tubercle and additional granules. Abbreviations: **b**, button; **c**, carina on sternite 4; **g**, G1; **gr**, granule; **tu**, tubercle; **4**, **5**, **6**, sternites 4, 5, and 6.

O. quadrata (Fabricius, 1787), *O. gaudichaudii* H. Milne Edwards *et* Lucas, 1843. The socket is vestigial or absent. In *O. pygoides* Ortmann, 1894 there is only a vestigial button.

In the large genus *Uca* Leach, 1814, which has been subdivided (Bott 1973; Crane 1975; von Hagen 1976), the configuration is variable. According to the species, there is either a button, small but acute, or a granular zone, or a longitudinal set of granules (with the anterior one more developed) located under the abdomen, but no differentiated socket is discernible. In the case of a unique button, it is not covered by the relatively long pleopods which are more medially situated. We use by convenience the nomenclature of Crane (1975) instead of Bott's names (1973) (see von Hagen 1976; Manning & Holthuis 1981: 224).

In *Uca (Afruca) tangeri* (Eydoux, 1835) there is generally a marked tubercle just behind the sternal suture 4/5, in a setose region, and sometimes one or even two additional granules are in the same row (Fig. 24D). In *U.* (*Uca*) *maracoani* (Latreille, 1802), along the external border of the sterno-abdominal cavity, the sternite 5 bears a set of arranged granules, which extend a little on to sternites 4 and 6 (additionally, a pair of small carinae is present on sternite 4, see below). In *Uca* (*U.*) *princeps* (Smith, 1870) the granules are larger and more numerous on the anterior part of sternite 5, which appears slightly elevated.

Species belonging mostly to the subgenus *Minuca* Bott, 1954 are characterized by an additional structure, called *crans d'arrêt* (safety catch) by Guinot (1979: 153). In *Uca* (*Minuca*) *vocator* (Herbst, 1804), *U.* (*M.*) *mordax* (Smith, 1870), *U.* (*M.*) *rapax* (Smith, 1870) (Fig. 26E) and in *U.* (*Boboruca*) *thayeri* Rathbun, 1900 (Fig. 24C) there is a rather setose, sometimes minutely granular area, a small tubercle well visible behind sternal suture 4/5, and a special structure that arises from a denticulated crest that encircles the end of the sterno-abdominal cavity. On each side, in the middle of sternite 4, this crest is prolonged internally by two short and smooth (under the binocular) carinae, which are practically horizontal but directed towards the slope of the cavity and penetrate inside the sterno-abdominal cavity. This pair of carinae corresponds to the limit between abdominal segment 6 and telson. It is suggested that, when the crab inserts its telson in the deep sterno-abdominal cavity (animals preserved in alcohol do not show any muscular tonus), the thickened anterior part of the telson is held by the carinae, which immobilizes the abdomen. All the *Uca* (*Minuca*) species that were examined possessed a pair of carinae.

Other *Uca* species have a similar pair of carinae, as in the case of *Uca* (*Celuca*) *pugilator* (Bosc, 1802) in which the carinae are thickened at their distal end. In *Uca (Celuca) urugayensis* Nobili, 1901 these carinae are markedly curved upwards.

Subfamily Heloeciinae H. Milne Edwards, 1852 (= Heloeciinae Türkay, 1983)

Heloecius Dana, 1851, considered as the most primitive genus within the family Ocypodidae, has been removed from the subfamily Ocypodinae to be placed in the subfamily Heloeciinae, in which the genus *Ucides* Rathbun, 1897 was also (at least provisionally) included (Türkay 1983; Fielder & Greenwood 1985; Tavares 1990). In *H. cordiformis* (H. Milne Edwards, 1837), an intertidal and burrowing crab active at low water in the mangrove, and *Ucides cordatus* (Linné, 1763), that occurs supratidally (Hartnoll, 1988), no button or socket was observed. In these two genera, the sterno-abdominal cavity is very deep and long, the G1 reach the level of sternite 4 (then covering the sternite), and the somites with the usual locking press-button (sternite 5 and pleomere 6) do not correspond. *Ucides* is notably distinguished by its abdominal segments 5 and 6 fused in a rigid plate, whereas *Heloecius* has a wider and normally segmented abdomen.

Subfamily Macrophthalminae Dana, 1852

In *Macrophthalmus* Latreille, 1829 (see Komai *et al.* 1995) a part of the species examined showed a tubercle, sometimes acute and always behind the sternal suture 4/5, and a shallow socket in the middle of abdominal segment 6. *Macrophthalmus* (*Venitus*) *latreillei* (Desmarest, 1822) (Fig. 24A) represents an example of an acute button, probably providing an effective locking mechanism. In *M.* (*Macrophthalmus*) *dilatatus* de Haan, 1835, the socket is positioned in the anterior part of the abdominal segment 6, and the apparatus seems to function. In *M.* (*Macrophthalmus*) *milloti*

Crosnier, 1965, *M.* (*Macrophthalmus*) *brevis* (Herbst, 1804), *M.* (*Macrophthalmus*) *consobrinus* Nobili, 1906 and *M.* (*Mopsocarcinus*) *boscii* Audouin, 1826, the system seems to be effective. Other macrophthalmine species have a system which appears weak and perhaps even inefficient. In *M.* (*Hemiplax*) *hirtipes* (Jacquinot, 1853) there is a button, but a socket is not perceptible under the binocular. In *M.* (*Mareotis*) *depressus* Rüppell, 1830, and *M.* (*Mareotis*) *banzai* Wanda *et* K. Sakai, 1989, the buttons become very minute. *M.* (*Mareotis*) *japonicus* (de Haan, 1835) has lost both parts, sternal and abdominal, of the locking apparatus.

Subfamily Dotillinae Stimpson, 1858
(= Scopimerinae Alcock, 1900)

In *Dotilla* Stimpson, 1858 the sterno-abdominal cavity is very deep, with well-defined margins. The abdomen is perfectly inserted in the cavity and its ventral part is almost completely covered by the swollen hindgut. In *D. myctiroides* (H. Milne Edwards, 1852), *D. fenestrata* Hilgendorf, 1869, *D. wichmanni* de Man, 1892, and *D. malabarica* Nobili, 1903 there is a minute prominence, very close to (almost on) suture 4/5, but no socket is discernible, at least under a binocular. In *D. sulcata* (Forskål, 1775) the suture 4/5 is thickened and slightly carinated, without a button, and no socket is perceptible.

In the two examined species of *Dotillopsis* Kemp, 1919, *D. brevitarsis* (de Man, 1888) and *D. profuga* (Nobili, 1903), the anterior segments of the abdomen are inserted in a relatively broad cavity, and the pleon is markedly constricted and well-inserted at the level of the basal part of segment 5. The posterior end of the abdomen is included in a deep and narrow sterno-abdominal cavity. No button or socket is visible.

In all species of *Scopimera* de Haan, 1833 that were examined, there is a small button behind suture 4/5 and a socket in the postero-lateral angles of abdominal segment 6. The mechanism is functional.

Family Camptandriidae Stimpson, 1858

A subfamily level was proposed by Stimpson (1858) but, for a long time, the genus *Camptandrium* Stimpson, 1858, was referred to diverse groups, being attributed to the Macrophthalminae within the family Ocypodidae (Balss 1957). Serène (1974) formally defined the subfamily Camptandriinae and included the genera *Leipocten* Kemp, 1915 and *Paracleistostoma* de Man, 1895, whereas at the same time Pretzmann (1974) established the "new" tribe Camptandriini. Manning & Holthuis (1981: 193, 348), who described five new West African genera, recognized the subfamily. Reviewing the genus *Baruna* Stebbing, 1904, Harminto & Ng (1991) emphasized the unique characters of the camptandriine group, in particular the unusually recurved G1. The taxonomy of the camptandriines, which consists of nearly twenty genera, was revised by Tan & Ng (1994) and Al-Khayat & Jones (1996), and awaits being raised to family status Camptandriidae (Ng 1998 and pers. comm.). The camptandriid crabs usually live in estuarine, especially mangrove habitats.

In *Tylodiplax* de Man, 1895 and *Baruna* Stebbing, 1904 there is a typical press-button, persistent throughout life. In *Shenius anomalus* (Shen, 1935) the sternal tubercle is acute, and the socket clearly visible. In *Paracleistostoma depressum* de Man, 1895, *Serenella leachii* (Audouin, 1826) and *Ilyogynnis microcheirum* (Tweedie, 1937) the button, situated close to the sterno-abdominal margin, varies from prominent to flattened, and the socket, situated on the edge and the whole length of abdominal segment 6, varies from slightly hollowed to flat.

The locking apparatus seems functional in all examined Camptandriidae.

Family Gecarcinidae Macleay, 1838

The male abdomen forms a relatively thin plate. On sternite 5, often covered with numerous setae, there is a prominence with an uneven surface; no abdominal socket is discernible, however. In *Gecarcinus lateralis* (de Fréminville, 1835) three male individuals measuring 22 × 30 mm, 39 × 32 mm, and 42 × 34 mm have two granules, one larger than the other, very close to suture 4/5; in a male individual measuring 46 × 36 mm the granules are fused and are not reached by the male first gonopods. In *G. planatus* Stimpson, 1860 (Fig. 25A, B) a large oblique prominence is located in the middle of sternite 5, with an un-

even and setose surface; no socket, however, is perceptible on pleomere 5.

In *Cardisoma carnifex* (Herbst, 1796), a male measuring 59 × 68 mm shows 2-3 granules very close to suture 4/5 in a setiferous zone; a male measuring 83 × 69 mm shows a granulous prominence plus a row of granules, the apex of G1 being just behind the granules. *Discoplax hirtipes* (Dana, 1852) follows the same pattern.

Epigrapsus politus Heller, 1862 displays a relatively strong and rugose button in the middle of sternite 5; the socket is visible because of its calcified border.

Gecarcoidea lalandii H. Milne Edwards, 1837 (male individual measuring 50 × 67 mm) shows a wide and rough prominence on the setiferous sternite 5, probably with particular microstructures, but no corresponding socket.

Family Mictyridae Dana, 1851

In *Mictyris* Latreille, 1806 (type species: *M. longicarpus* Latreille, 1806) the sterno-abdominal cavity is not deeply hollowed and its margins are not well-defined laterally. The abdomen is long, particularly wide and expanded, except for the small telson; its anterior segments are tightly inserted between the P5 coxae and sternite 8 (Guinot 1979a, fig. 29C). In addition, in *M. longicarpus* an oblique protuberance on each side of sternite 8, just behind the suture 7/8, props up the pleomere 2.

The five species of *Mictyris* that were examined do not have a sternal button or an abdominal socket. In the males (no female was observed) of *M. platycheles* H. Milne Edwards, 1852, two long lateral projections arise from a crest on sternite 4 (Fig. 25C, D). The latero-external parts of pleomere 6, with no visible differentiated zone, lean on the pair of projections, and the telson loosely moves between these two strong structures.

The crest on sternite 4 is without projections in mictyrids, except in only one species, *M. platycheles*. It is evident that the pair of projections in *M. platycheles* is not homologous with a locking apparatus of the press-button type: the telson is simply received in the space between the two projections. Apparently lateral displacements of the abdomen will be prevented due to the pair of projections that guides the course of the telson.

GENERAL DISCUSSION

When observing living crabs or specimens preserved in alcohol and when referring to published data, it is rare, if not exceptional, to find individuals with their abdomen not fixed to the ventral surface. A retained abdomen is the rule for males and also for prepubertal females, while the mature females acquire a wide abdomen that (usually) cannot be held to the thorax any longer.

Male and female abdomens

Male and female abdomens have initially six distinct segments, all loosely articulated, plus the telson. There is a tendency toward fusion of two or several pleomeres in a more rigid plate, sometimes with the sutures no longer visible.

The abdomen is capable of strong flexion and its ventral folding varies from weak to complete. The first segments are not completely flexed under the cephalothorax even in certain advanced crabs (Guinot 1979a, fig. 1H, I). The abdomen may be long, entering the bases of the Mxp3 and in great part folded, as in the Homolidae, or very short and incompletely flexed under, as in the Raninidae. The ventral inflexion of the abdomen is not an exclusively brachyuran condition, since it occurs in other Decapoda with a crablike facies (Porcellanidae for example). In Decapoda an elongated abdomen may be regarded as the plesiomorphic condition, versus a short and flexed abdomen in the apomorphic condition. But the developed, unprotected and unsegmented abdomen in paguroids, which contains almost exclusively the reproductive system, differs not only from that of other anomurans but from that of decapods in general (McLaughlin 1980: 150, figs 47A, 50A). The long abdomens, as well as the short, well-calcified (with symmetrical or more or less asymmetrical tergal plates) and folded abdomens, are not similar among the Reptantia.

In the Brachyura, plesiomorphic character states are the narrow tergal part of abdominal segments accompanied by elongated lateral pleura and a long telson, both found in Homolodromiidae (Guinot 1993a, 1995). For Scholtz & Richter (1995), the "original" decapod telson is triangular and pointed posteriorly; it is wide, more or

less square-shaped and posteriorly rounded in their Eureptantia, and it remains relatively wide and rounded in primitive brachyuran taxa such as Dromiidae [note that the telson is not square in Homolodromiidae]. Scholtz & Richter concluded (p. 298) that the triangular telson found in

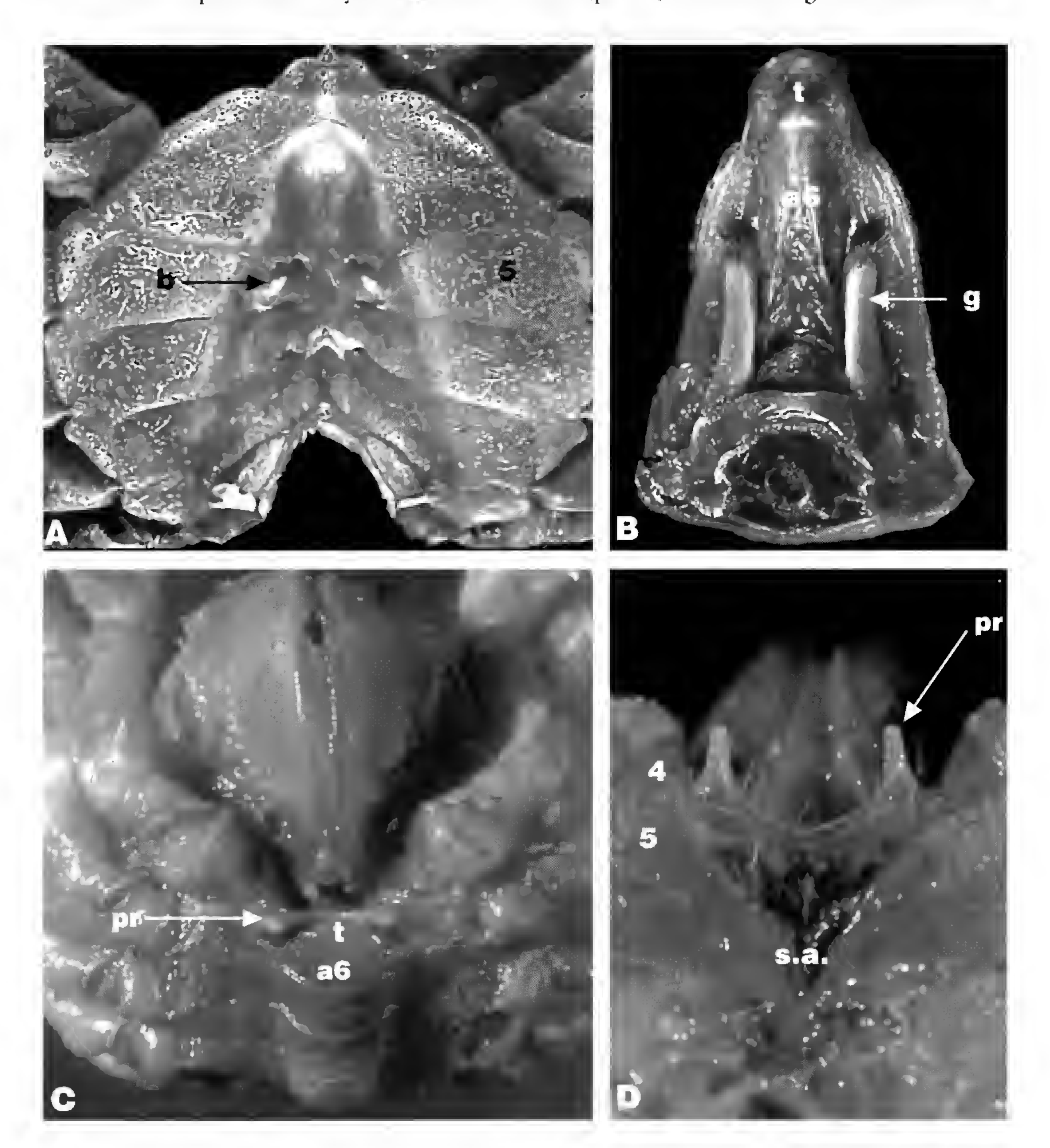


FIG. 25. — Locking apparatus in Gecarcinidae and Mictyridae; **A**, **B**, *Gecarcinus planatus* Stimpson, ♂ 53 × 77 mm, Lower California (MNHN-B 13154): **A**, thoracic sternum, without abdomen; **B**, ventral surface of abdomen, without discernible sockets; **C**, **D**, *Mictyris platycheles* H. Milne Edwards, ♂ 13.3 × 12.3 mm, Australia (MNHN-B 16086): **C**, ventral view; **D**, detail of the crest on sternite 4 with two projections. Abbreviations: **a6**, abdominal segment 6; **b**, button; **g**, G1; **pr**, pair of projections on sternite 4; **s.a.**, sterno-abdominal cavity; **t**, telson; **4**, **5**, sternites 4 and 5.

most crabs can be regarded as "a secondary alteration perhaps related to the reduction of the pleon and the loss of the tail fan."

In Podotremata, the plesiomorphic nature of the male abdomen is demonstrated by the presence of pleopodal (biramous or uniramous) rudiments on the somites 3-5 (most Homolodromiidae, all Dynomenidae, and a few Dromiidae). These same three families are characterized by presence of vestigial uropods, which are represented either by dorsal plates (all Dynomenidae, most Dromiidae) or ventral lobes (all Homolodromiidae, and a few Dromiidae) (McLay 1993; Guinot 1993a, 1995). In the other podotreme groups (Homoloidea, Cyclodorippoidea, Raninoidea, *i.e.* the Archaeobrachyura Guinot, 1977) and in all members of the Heterotremata-Thoracotremata assemblage, there is neither a trace of vestigial pleopods on somites 3-5 in males, nor a trace of appendagelike, platelike or lobelike uropods in both sexes (Table 3). The persistence of pleopods as rudiments on abdominal somites 3-5 in males could be regarded as related to the presence of vestigial uropods. In most of the Brachyura, the male abdomen becomes limbless, except for gonopods 1 and 2.

In Brachyura, the role of the abdomen is very different in the two sexes. Since the first two pairs of pleopods change (relatively) little at puberty in males, growth of the male abdomen is approximately isometric throughout. The female abdomen shows marked positive allometry in the juvenile phase and a large increase in size at the puberty molt, which brings it to a functional size when it is required. Compared to the chelae in males which continue to grow, the female abdomen is not an independent effector but can operate only together with the sternum. Having attained an effective size at the puberty molt, the abdomen reduces its allometric growth, since any further disproportionate increase would for example make walking difficult (Hartnoll 1982: 173). The female abdomen, in conjunction with the sternum, encloses a chamber that facilitates the fixation of the eggs to the pleopods and their protection during incubation. In many groups, during incubation, ovigerous females do not have their abdomen held closely against the thorax because it is displaced by the egg mass.

Sterno-abdominal cavity

In brachyuran crabs the thoracic sternum maintains the ancestral metamery, at least in the region formed by somites 4-8, that is, corresponding to thoracopods 4-8 (= pereiopods 1-5). The sternal plate, which shows an isometric growth (Drach 1959; Guinot 1979a), constitutes an essential part of the organism for phylogenetic studies. In accordance with configuration of the sternal plate, two major groups may be distinguished: the Podotremata and the Heterotremata-Thoracotremata assemblage.

In Podotremata, the arthrodial cavities of the pereiopods are not aligned (but, as in all Brachyura, they open laterally, instead of ventrally in macruran forms) and the sternum shows at least two different planes, the posterior part being tilted. The abdomen more or less fills up the entire width of the sternal plate, generally covering the space between the coxae of pereiopods, sometimes extending over bases of the coxae, and is rarely narrower than the sternal plate (Dynomenidae, Latreilliidae). There is not a true sterno-abdominal cavity, with defined margins, in most podotreme males. In the family Dynomenidae, a slight sternal depression, without defined borders, receives the rather wide abdomen. Exceptions in the Podotremata are the Cyclodorippoidea, which have a relatively wide sternal plate, and also the (fossil) Dakoricancroidea.

In podotreme females, a strong modification of the ventral surface occurs, with inclination of the coxae and modification of their internal surface, to form a wider space to receive the increased abdomen: this coxal zone becomes completely smooth and naked.

In the Heterotremata-Thoracotremata assemblage, the whole sternum tends to form a plate in the same plane (the arthrodial cavities of thoracic pereiopods 1-5 are aligned) and to widen, sometimes extensively. Metamery varies from having all sutures 4/5 through 7/8 parallel and complete in a narrow plate (plesiomorphy) to being more or less oblique and becoming partly or completely interrupted in a broad plate (apomorphy). The ventral surface is excavated by a special depression, with a shape that (more or less) corresponds to the abdomen. The abdomen folds down on it, completely covering the vulvae and pleopods,

except for rare cases. In the Thoraco-tremata, male sternal apertures also are covered.
Two synapomorphies of the Heterotremata-Thoracotremata assemblage are: presence of a sterno-abdominal cavity with defined borders (present, however, in certain Cyclodorippoidea and in Dakoticancroidea); presence of a press-button, which is typical and remains practically unchanged in all eubrachyuran crabs.

CARCINIZATION

In the process of carcinization (Borradaile 1916; Türkay 1986; Macpherson 1988; Lemaitre & McLaughlin 1995; Poupin & McLaughlin 1996; McLaughlin 1997) which leads to the crab-like form, *i.e.* the derived condition, diverse trends are correlated: reduction of the relative length of cephalothorax, specially broadening of the carapace, front, buccal frame, branchial cavity, and sternal plate; reduction of the rostrum; folding of the antennules and antennae; general flattening of the cephalothorax leading to cephalic condensation with the sensorial organs in the same plane, and with modification of orbits and eyestalks; reduction and folding of the abdomen and fusion of diverse pleomeres; partial loss of metamery on dorsal surface of the carapace and more significantly on the ventral surface; loss of pleopods (except for pairs 1 and 2) in males and of caudal furca in both sexes. Locomotion is no longer provided by the abdomen but assumed by the thoracic pereiopods. The strong reduction of the abdomen and its "integration" to the body modifies the center of gravity of the animal. The thoracic sternum broadens and forms a hard horizontal plate in a sort of shield, that in a way parallels the dorsal carapace. In the medial part of the sternal plate, the excavation of a cavity, with delimited margins to receive the abdomen, constitutes an essential evolutionary step of carcinization.
Intercalation of a wide sternal plate between the bases of the legs induces a greater distance between the P5 coxae and gonopods, with the effect that the coxal sexual male openings (and penes) become far removed from the foramina at the bases of the gonopods. The moving (migration) of male gonopores to a sternal position, close to the median axis in the vicinity of gonopods, is a derived condition within the Brachyura as a whole and also within certain families.
Depending on the transformation of the cylindrical shape to broad/compact and conical and increasing thoracic muscular mass, the endophragmal system significantly changes, its new organization contributing to the consolidation of the whole thorax, with concentration at the apex of its muscular attachment to, or suspension from, the carapace (Secretan in press). As a consequence of the reduction of the abdomen, the functional removal of the impeding abdomen, and as soon as all internal readjustments were completed with efficient reconsrruction of the skeleton, enables a vast improvement in the mechanism of locomotion. These adjustments, that were overcome already in the Dromiacea, have produced the highly successful brachyuran group, whose bodies are adapted for efficient walking and running (Bauer 1989: 64, fig. 18). It is a matter of fact, the Brachyura show strong adaptative radiation and dispersal to terrestrial and freshwater habitats (Glaessner 1957).

BRACHYURAN RADIATIONS

The three highest taxonomic units proposed by Guinot (1977), which express by their names the change in the position of gonopores, correspond *grosso modo* to the principal radiations in the Brachyura and can be documented paleontologically from the beginning of their existence at least in the Early Jurassic to the present.
The Podotremata became diversified in Middle and Upper Jurassic sediments. Their actual representatives are all marine, often inhabit deep waters and show a common tendency toward carrying behaviour with the last pair(s) of legs (Guinot *et al.* 1995).
A remarkable synapomorphy distinguishes all other crabs, that is, the Heterotremata-Thoracotremata assemblage: innovation of the female gonopores on the sternal plate, the vulvae, and loss of isolated spermathecae (Tavares & Secretan 1992).
The most diverse groups of crabs, the Heterotremata, most of which survive to the present, is a product of Late Cretaceous-Early Tertiary. Their actual members show full development of all locomotory pereiopods (except for the Dorippoidea and other small other groups such as

retroplumids and palicids). They are generally marine. Are excepted the true freshwater crabs: the diverse families and all representatives are heterotreme. It is to be noted that the families Hymenosomatidae (with some members adapted to freshwater environments), Goneplacidae, Hexapodidae, Pinnotheridae, and Cryptochiridae were recently attributed to the Heterotremata (Guinot & Richer de Forges 1997, table 1).
The remaining crabs belong to the Thoracotremata, which are known from the Cenozoic. On account of the last revision of the classification by Guinot & Richer de Forges (1997), they are almost entirely composed of littoral and terrestrial species, all distributed in five families: Grapsidae, Gecarcinidae, Camptandriidae, Ocypodidae, and Mictyridae. They are justly the forms which have successfully exploited a variety of aerial environments, with all necessary adjustments in physiology, behaviour, reproductive and developmental strategies (Bliss 1968; Burggren & McMahon 1988). They are the result of complete carcinization allowing advantageous locomotory adaptation such as fast running, prolonged walking on land (migration), tree-climbing, burrowing. Thus it is noteworthy that the classification based on morphological characters fits with the ecological and behavioural (ethological) habits. Because of their recent appearance the Thoracotremata have had relatively little time for radiation and probably exemplify only the early stages of evolution of their terrestrial competence.

Abdominal retaining by the limbs

In the podotrematous families Homolodromiidae, Dromiidae, Homolidae, and Poupiniidae, abdominal retention (when existing) is achieved by diverse means that involve various appendages (Mxp3, P1-P2, sometimes even P3). The structures overhang the abdomen or are coaptated with its margin (Tables 1, 2), prevent it being lifted up. In addition to retention by the limbs, the Homolidae and Poupiniidae display a press-button system (homolid press-button): both systems may act simultaneously. But, in the more advanced homoloid family Latreilliidae, retention by the coxae of appendages was lost, and only the press-button system is effective.
In the family Dynomenidae, only primitive representatives have their abdomen restricted in its lateral movements by coxal structures of the second pair of pereiopods. The more advanced dynomenid species similarly restrict sideways movements of their abdomen but by a sternal structure.
The Raninidae have no retaining apparatus. An exception is the subfamily Lyreidinae, where the pereiopods do not play any role: instead a sternal structure arising from sternite 5 acts with a socket on pleomere 6.
In the Cyclodorippoidea, which possess a relatively wide sternal plate and have their abdomen far removed from the coxae of the pereiopods, the appendages are never involved. Special retaining devices, with structures located on the sternum, exist in the families Cyclodorippidae (coaptation by engagement) and Phyllotymolinidae (block system).
In specializing the brachyuran model, the evolutionary process has provided an abdomen that is far removed from the coxae of the pereiopods and is completely placed on the wide sternal plate. This results in a "migration" of retaining elements on to the thoracic sternum, and particularly from P2 coxa on to sternite 5 (a transformation series found within the family Dynomenidae). Thus is explained the emergence of a pair of prominences on the sternite corresponding to P2, *i.e.* sternite 5.
In the advanced Podotremata and all Eubrachyura, the thoracopods are no longer involved: they become free from all functions other than locomotion and may be active for other purposes.
In the Podotremata that are considered as the most primitive; viz. Dromiacea and Homoloidea (except Latreilliidae), the abdomen is retained by thoracopods (Mxp3 through P3), movements of which are very important in that retaining system. At the level of P2-P3 the thoracic sternum presents characteristic depressions, already observed in the Homolodromiidae. These sterno-coxal depressions (Guinot 1995) allow coxae of the legs to easily slip inside during their movement and to swivel up on their condylar articulation with increasing amplitude.
Sterno-coxal depressions are present in all

Homolodromiidae, Dromiidae (exceptions are very rare: *Pseudodromia, Ascidiophilus*), all Dynomenidae, all Homolidae, and in the Poupiniidae (Figs 5D, 7A, 7D, 9C). It is remarkable that they are absent in the Latreilliidae, where the pereiopods do not play any role and the fixation is exclusively secured by the press-button on sternite 4 (Fig. 9D). Sterno-coxal depressions also lack in all brachyuran crabs in which pereiopods are no longer involved in retaining, that is in all Eubrachyura. A conclusion may be drawn: a strict correlation exists between the involvement of pereiopods (P2-P3) and the presence of such sterno-coxal depressions, exemplified by the different patterns found in the two related families Homolidae and Latreilliidae.

Modifications occur in the abdomen in relation to the retaining apparatus by the limbs. Abdominal segment 6 may be markedly modified. On the one hand, in Podotremata it is directly in contact with a differentiated structure on the pereiopods: either it is remarkably constricted, for example in *Dromia monodi* (Fig. 3A), or its external edge is thickened and hollowed for example in *Lauridromia dehaani* (Fig. 2A, B), *L. intermedia* (Fig. 2C), *Hemisphaerodromia monodus* (Fig. 3C, D), and *Exodromidia spinosa* (Fig. 5D). On the other hand, a transformation occurs when the appendagelike uropod becomes a sexually dimorphic dorsal plate (most Dromiidae, all Dynomenidae) and particularly when it has evolved into a socket, which is a major event (Homoloidea, Lyreidinae, practically all Eubrachyura) (see Hypothesis about the homology uropod-socket). The telson also may be significantly modified: for example the deep notch on its external edge in the dromiid *Lauridromia dehaani*, the long and sexually dimorphic spine at its tip in the dromiid genus *Exodromidia*, its base (pleotelson) with a very thin edge in the cyclodorippid genus *Clythrocerus*. In the Homoloidea the telson plays a tole in abdominal retention and is inserted between maxillipeds: it is either overhung by (Fig. 8D) or fits into Mxp3 (sometimes there is a combination of these two modalities), with modifications occurring in its general shape and on its external margin (Figs 8B, C, 9B).

FASTENING AND UNFASTENING

The musculature of abdomen, well studied in *Cancer pagurus* (Pearson 1908), in *Carcinus maenas* (Daniel 1931) and in diverse species (Abrahamczic-Scanzoni 1942), consists of a pair of dorsal extensor muscles and a pair of ventral flexor muscles for each segment. The musculature pattern depends on the number of segments, either all free or diversely fused, and also varies with respect to sex. In crabs with a press-button, the abdomen is attached at the level of pleomere 6, which limits general movement of preceding segments. The telson alone, sometimes very movable, is capable of freely moving around its articulation with pleomere 6. This configuration enables the telson to be moved alone, for example while defecating, since the anus opens on the telson (for a discussion on telson and anal segment, see Schram 1986: 7).

In the literature concerning brachyuran crabs, cases of unfolded or extended abdomens are generally only mentioned during mating. In the course of their numerous experiments on living *Pachygrapsus marmoratus* and *Carcinus maenas*, respectively, Vernet-Cornubert (1958) and Démeusy (1958) (who took the locking systems into account in the two sexes) do not indicate cases of unfolded abdomen except for the mating process. When the abdomen is experimentally unfastened, action to refasten it on to buttons is not immediate; in *Carcinus maenas* it needs a few seconds to two hours (Kollmann 1937: 80).

It is obvious that, in the natural posture, probably the resting position, the abdomen is closed and attached to the thoracic sternum. The question is to know whether mature males unfasten their abdomen at a time other than the mating process (including pre- and post-copulatory periods) and also for the exuviation. The young male and the female before the moult of puberty perhaps do not need to move their abdomen for any purpose. In fact the abdominal flexing is poorly studied in the Brachyura.

Abdomen flapping in males is, to our knowledge, generally reported at the period of copulation (Watson 1970, 1972; Hiatt, 1948; Hinsch 1968). Laboratory observations on mating behaviour of *Chionoecetes bairdi* indicate that the crab may repeat several times the action of lowering its

abdomen, holding it open for a few seconds and then flexing it upward to a fully closed position (Donaldson & Adams 1989: 44, tables 1, 5). These authors report that males and females normally flap their entire abdomen while defecating. But a movement of the telson alone might be sufficient. Movements involving abdomen extension are probably required during the procedures of species recognition and courtship. It is not surprising that, at least in certain species, flapping is an action performed during reproductive behaviour. For example periodic flexing of the male abdomen was observed during the grasping of females in *Chionoecetes opilio* (Watson 1970: 1612). It was demonstrated that sacculinized *Rhithropanopeus harrisii* (Gould) showed an abdominal flexing response when exposed to certain peptides, similar to the pheromones released by the eggs just before hatching (de Vries *et al.* 1989). Rhizocephalan-parasitized *Hemigrapsus sanguineus* (de Haan) flex their abdomen with a waving action, while the sacculinid releases nauplii (Takahashi *et al.* 1997: 159).

Flapping has another function in mature and ovigerous females (Bauer 1989: 66) than in males, and special pheromones seem to induce abdominal flapping in ovigerous females. It may be asked whether abdomen fixation is permanent for prepubertal males and females. It was hypothesized, already by Pérez (1928a: 462), that females of *Carcinus maenas* naturally unfasten the abdomen during the moult, notably at puberty moult, just before mating (the male attends the female until she moults, after which they mate immediately). This is effectively possible in all species in which mating females mate only while soft, as in *Carcinus*. In the case where a hard female mates, the mature female does not need to unfasten its abdomen since it is not fixed. A similar behaviour pattern, viz. an active involvement for abdomen detachment, is necessary for males of all brachyuran crabs since they copulate only while in the fully hardened condition (Hartnoll 1969). The only way to fasten and unfasten the abdomen seems to be by a postero-anterior movement. In living crabs the experimental unfastening is generally very difficult.

In leucosiids, the abdomen adheres to the sternal plate in males and, to the highest degree, in mature females. Its detachment probably necessitates a physiological mechanism when copulating with a hard female, perhaps a local decalcification (Drach 1939, 1955, unpublished data). Hartnoll (1969: 168) indicates that, in *Philyra*, copulating females are presumably not very recently moulted: when the female "eventually extends her abdomen he [the male] rapidly moves so as to face her, and mating occurs."

The abdomen, in conjunction with the sterno-abdominal cavity, serves to cover (with some rare exceptions) the first two pairs of gonopods, which act for the sperm intromission during copulation, and the female pleopods before the puberty molt. It provides a protection for the apertures of spermathecae in the Podotremata, for vulvae in the Eubrachyura (with some rare exceptions), and generally for the penes, either coxal or sternal. It is clear that inclusion of the abdomen between the pereiopods or in a special cavity obviates its possible impeding movements during swimming, burrowing or walking. In the great majority of specimens examined the sterno-abdominal cavity was clean, which certainly proves a perfect seal. Brachyuran crabs lack general body cleaning but still remain quite clean (Bauer 1981, 1989).

The case of the family Leucosiidae

In leucosiids such as *Leucosia* a first consideration is the absence of any socket on abdominal segment 6 (Fig. 19D). This pleomere is very elongate and has its whole length located on sternite 4. The abdomen is fixed by a system that conspicuously differs from the typical press-button. The sternite 5 is prolonged into a spur that perfectly enters a notch of the abdominal margin between segments 5 and 6. The spur is often completed by analogous protrusions of sternites 6 and 7. The leucosiine spur appears as an autapomorphy for the most advanced leucosiid taxa. It would be interesting to verify whether simple coaptations by engagement (Fig. 18) found in primitive representatives (Ebaliinae, Cryptocneminae, Philyrinae *pro parte*) are correlated to coxal male gonopores and whether a coaptation by assemblage with a spur tends to occur in advanced representatives with coxo-sternal male gonopores (Philyrinae *pro parte*, Leucosiinae, see the penis in

Fig. 19C, *p*). It is noteworthy that this particular kind of coaptation occurs in the advanced family Leucosiidae, characterized by a pronounced cephalic condensation.

FAILURES, LOSS OR ABSENCE OF HOLDING APPARATUS

The absence of a morphological holding apparatus is rare in Brachyura.

Certain Podotremata do not present any special holding structures. Our investigations, however, have shown the existence of some particular devices. The shell-carrying *Hypoconcha arcuata* and *H. panamensis* and the Cymonomidae have their abdomen simply bent at right angles, with only its posterior part being normally applied against the ventral surface. Burrowing Raninidae have a very short abdomen: anterior segments are in prolongation with the carapace and the posterior ones not flexed, which does not allow a fastening. Nevertheless a firm locking is found in the subfamily Lyreidinae (Fig. 11), the abdomen of which is a little longer, narrower, and better included between the legs than in other raninid subfamilies.

Some Heterotremata lack a locking press-button or show a dysfunction of the mechanism (Table 3). This essentially concerns crabs having a narrow thoracic sternum, with sutures 4/5 through 7/8 *grosso modo* parallel and continuous, and with a developed median line. Their sterno-abdominal cavity is either absent or hardly/weakly defined. This configuration appears to be related to the character state "short abdomen", that gives rise to a gap between the two parts usually involved, *i.e.* sternite 5 and pleomere 6. A remarkable consequence in females is that the vulvae remain exposed on the sternite 6. The putative consequence manifests itself in diverse manners:

Case 1. No apparent structures (no buttons, no sockets): *Corystes*, *Pseudocorystes*, *Jonas*, and *Gomeza* (but, at least in *G. bicornis*, a very short sterno-abdominal cavity is present posteriorly, and closing is provided in particular by a bending of the posterior part of the abdomen). These four genera belong in the family Corystidae (Fig. 12A, B, D, E).

Case 2. Presence of acute and posteriorly directed hooks close to suture 5/6, but located so far from the abdomen that locking is not possible: *Nautilocorystes* (Fig. 12C), which belongs in the Corystidae. Absence of sockets in postlarval forms and in juveniles needs to be confirmed.

Case 3. Presence of both differentiated sternal tubercles and abdominal sockets. But in certain variably sized adult individuals a non-correspondence occurs between the two parts, that became separated by a gap: *Atelecyclus rotundatus* (Fig. 13A, B), and *Peltarion* (Fig. 14A). The mechanism was effective only in some of the individuals. The loss was apparently not related to size as shown by examining about thirty male specimens. *Atelecyclus* and *Peltarion* belong to the primitive family Atelecyclidae, in which a true sterno-abdominal cavity, however, is present (unlike the Corystidae).

Case 4. Asymmetry in disposition caused by a gap between the two structures on one side of the body. In *Trachycarcinus* (Fig. 13D) the mechanism generally functions, but a dysfunction occurs in old male individuals with one heavy chela.

In addition, the case 1 is also found in crabs in which the thoracic sternum widens, with all the sutures interrupted: Orithyiidae. A sterno-abdominal cavity is present, which is elongated but not covered by the short abdomen, so that the vulvae remain exposed in females.

The case 2 is also found in crabs having a wider thoracic sternum, with all the sutures interrupted, but with a "too short" abdomen: *Bellia picta* (Fig. 14B, C) in the family Belliidae. Despite the presence of both prominences and sockets, there is no possibility of locking. It is to be noted that the mechanism works in young females. The vulvae are always exposed in females of this species. The non-coincidence of the locking structures occurs in the shorter abdomen of *Bellia*, that is, in the most primitive representative of the family Belliidae and a typical burrowing form. The two other genera of the family (*Acanthocyclus* and *Heterozius*), with a well-excavated sterno-abdominal cavity, a longer abdomen, and "normal" vulvae, have a functional press-button: they are more carcinized and advanced forms, not so specialized for burrowing activity (note that *Heterozius* is free-living but often is found deeply burrowed under boulders, C. L. McLay pers. com.).

In the family Thiidae, also rather primitive, the abdominal locking does not seem to be very firm.

In conclusion, the primitive condition in all the preceding families is confirmed by the failure of the locking system (complete or partial absence of structures or non-correspondence between sternal and abdominal structures), even at the individual level. This plesiomorphic state seems to mainly characterize burying or burrowing heterotrematous forms.

In the Pinnotheridae a press-button was observed only in hard-shelled stages, that may bear a large knob on sternite 5 and a smaller one on sternite 6, which is very unusual; the soft-shelled stage seems to be devoid of any morphological structures. In the Cryptochiridae, or gall crabs, no trace of an apparatus is visible. That recalls the commensal dromiids *Pseudodromia* and *Ascidiophilus* (their body is enclosed in an ascidian) where also lacks an abdominal retaining mechanism. Absence of any morphological apparatus seems to be related to the protection afforded by the host.

A crucial question is to determine where the press-button has been established in the heterotreme lineage, since sternal prominences combined with sockets are an innovation of the Eubrachyura (for the case of the Homoloidea and the Lyreidinae, see below). An investigation of corystid and atelecyclid fossil genera probably would give good results concerning the common ancestor. It is likely that the ancestral condition in corystids was with a complete apparatus.

Within the Thoracotremata, the press-button is very efficient in diverse groups (Grapsinae, Plagusiinae, Camptandriidae for example) but tends to become reduced, obsolete and non-fonctional (Varuninae, Sesarminae), or completely disappears in the most advanced taxa (essentially in the Ocypodidae). The abdomen is no longer fastened but, however, remains applied against the sternal plate in the rather deep sterno-abdominal cavity.

The most primitive Thoracotremata are the grapsid subfamilies Grapsinae and Plagusiinae, with the male gonopore adjacent to the P5 coxa (Guinot 1979a, fig. 52A-C): they have an efficient press-button. All of them are truly marine forms, either shore crabs (rock crabs) or largely aquatic (*Percnon*), with the exception of some *Geograpsus* species which show terrestrial adaptations. The monophyly of either of these two families is well-supported by their locking systems (the status of certain grapsine genera perhaps needs to be re-evalutated).

The Sesarminae, in which the proximity of the gonopore varies from very close to P5 coxa to rather far away (Guinot 1979a, fig. 52D, I, J), have a press-button which is either normal and effective or inefficient beyond a certain size, or completely lost. The Varuninae, in which the gonopore is more or less far on sternite 8 (Guinot 1979a, fig. 52F-H), obviously do not form a monophyletic group: many representatives show a press-button which tends to be lost. It would be interesting to compare the reduction/loss of the locking systems with regard to the lifestyle (Burggren & McMahon 1988).

In the Camptandriidae (Guinot 1979a, fig. 53C), that certainly is a monophyletic group, the press-button configuration is very homogeneous, with an effective mechanism that persists throughout life in males; note that their pleopods are not very chitinized.

The Gecarcinidae, with a gonopore either close to the P5 coxa or only a little away (Guinot 1979a, fig. 54A-D), may show a button but no defined socket. It is noteworthy that *Epigrapsus politus*, which has a less terrestrial habitat than the rest of the family, has a strong apparatus in contrast with the others where the locking is not effective.

The Ocypodidae, in which the gonopore is sternal and in relation to suture 7/8 (Guinot 1979a, figs 53A, B, D, 54E), are more advanced than Grapsidae. The Macrophthalminae and the Dotillinae (= Scopimerinae) have a press-button which is more or less efficient, depending on genera/species. In contrast, the Ocypodinae, some of which have vestigial but inefficient buttons, and the Heloeciinae seem to never retain their abdomen by this device. *Uca* also seem to have, at least in the examined preserved material, their abdomen only loosely applied. The pair of carinae on sternite 4, that characterizes the subgenus *Minuca* for example, constitutes a new kind of apparatus. In Mictyridae, in which locking by a press-button is

no longer possible (Guinot 1979a, fig. 29), the large abdomen seems to be not firmly retained, even in the species (*Mictyris platycheles*) which develops a new kind of retention on sternite 4 that restricts lateral movement of the abdomen in its posterior part.

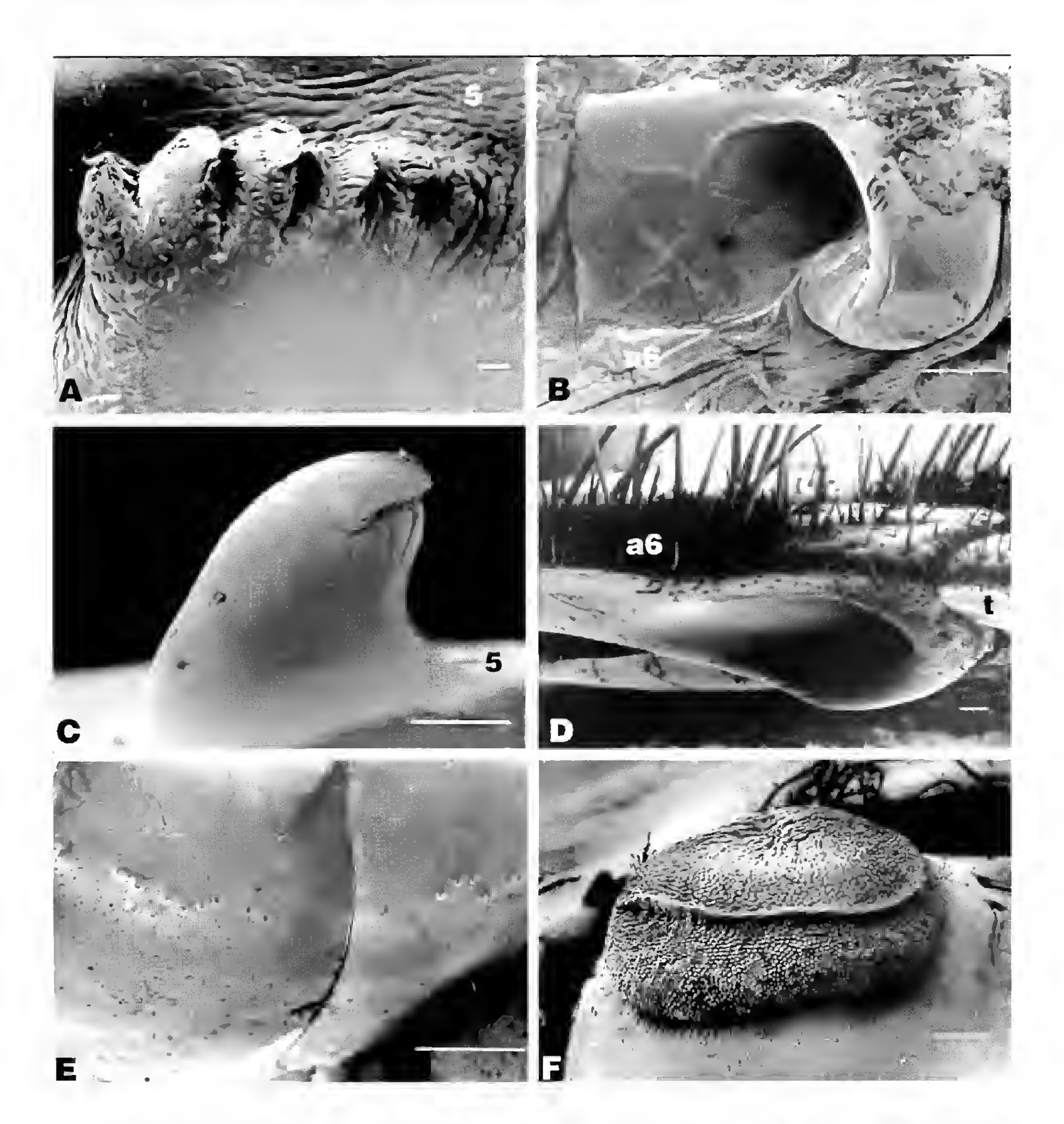


FIG. 26. — Photographs with the scanning electron microscope; **A**, **B**; *Pinnotheres pisum* (Linné), ♂ 4.7 × 4.6 mm, at the hard stage, La Rochelle (MNHN-B 10604); **A**, button; **B**, socket; **C**, **D**, *Austinograea alayseae* Guinot, ♂ 25.3 × 39.6 mm, Pacific Ocean, Lau back-arc Basin, BL 10, 1750 m (MNHN-B 24055): **C**, button; **D**, socket; **E**, detail of the granular zone on sternites 5 and 6 of *Uca* (*Minuca*) *rapax* (Smith), ♂ 15 × 23 mm, West Indies (MNHN-B 22540); **F**, button of *Plagusia immaculata* Lamarck, ♂ 29.1 × 30.7 mm, Pondichery (MNHN-B 11702). Abbreviations; **a6**, abdominal segment 6, **t**, telson; **5**, sternite 5. Scale bars: A, 10 µm; B-D, F, 100 µm; E, 1 mm.

This suggests the following remark. The Thoracotremata forms that became independent from the sea (including those occurring intertidally but with frequent aerial exposure, or living supratidally, or being adapted to life on land) show a trend not to fix their abdomen by a press-button apparatus and to replace it with another system.

Microstructure

Investigations with the scanning electron microscope are in progress (J.-M. Bouchard) with the aim to point out the presence of microstructures on sternal prominences and sockets. At the present time, with a sample of representatives taken from about fifteen brachyuran families, a great variety of microstructures has been discovered on the buttons, differing in relative size, orientation, general shape, detailed morphological features, ornamentation, and setae. These preliminary results permit the following first comments.

The microstructures of the sternal prominences might represent a valuable criterion at the generic level (for example in the Lyreidinae they distinguish the two genera *Lyreidus* and *Lysirude*), and hypothetically at higher levels. They are an indicator of sex (being present in males and becoming modified in females), puberty moult (at least in females), and the age of individuals. For example in *Lysirude channeri* the hooks of the locking projections are well-developed in males and blunt or even obsolete in females (Fig. 11C, D). The variety of patterns shown by the prominences is exemplified by Figs 10D (Homolidae), 26A (Pinnotheridae), 26C (Bythograeidae), and 26F (Grapsidae Plagusiinae). It is obvious that microstructures improve the contact between involved surfaces, enhance the assemblage of both parts and increase efficiency of the locking mechanism. It is noteworthy that microstructures were observed as well among the Podotremata, in the Lyreidinae (sternal projection from sternite 5) and in the Homolidae (homolid press-button on sternite 4), as in the Heterotremata-Thoracotremata assemblage (typical press-button on sternite 5). These microstructures might be accepted as valid indicators of phylogenetic affinities, *i.e.* synapomorphies, except if they are suspected of reflecting convergence.

Investigations concerning the microstructures of the sockets might similarly be taken into account: different patterns in orientation, shape, and depth have already been observed (Fig. 26B, D).

The abdominal retaining mechanism as a phylogenetic criterion

The determination of what might be the primitive or advanced mode of abdominal retaining mechanism among Brachyura is basically a matter of functional character polarity assessment. The method of outgroup analysis is not informative. In advanced Decapoda a general trend toward protection of abdomen is observed. "Macruran" forms and some galatheid possess strongly calcified abdominal tergal plates; paguroids have their long and soft abdomen sheltered inside a gastropod shell or protected inside wood; crablike porcellanids, lithodids and lomoids show abdominal reduction and flexion beneath the body, without any apparent retaining structures. In contrast, brachyuran crabs fold their reduced abdomen and obviate its possible impeding movements in two basic ways: a holding by the thoracopods and/or a locking by a press-button system (homolid press-button and typical press-button).

In utilizing the method of ingroup analysis, holding by the limbs would indicate that this mode of operation is the most primitive. In Podotremata the retaining type that is used, with its detail, may offer a reliable criterion in recognizing podotreme families. Careful study of the evolution of the form of both sockets and buttons, with uniformity in general shape, position, and function indicates that the press-button is a very successful mode of abdominal holding. This uniformity within the wide diversity of bodies in the Eubrachyura probably shows that the press-button is the most efficient use of their energy resources in order to achieve locomotion, reproduction and other functions. The retaining or locking mechanism is an almost constant feature in Brachyura. Its absence in diverse advanced Thoracotremata is considered to be the result of a secondary loss: its replacement by an alternative method remains to be explained.

In the Podotremata a sternal differentiation evolved independentely in several lineages: dynomenid, homoloid, lyreidine, cyclodorippoid (cyclodorippid and phyllotymolinid).

Some of the dynomenids (*Acanthodromia*, *Paradynomene*, *Dynomene* pro parte exemplified by *D. tanensis*) have coxal structures on P2 (plesiomorphy), but several of them (typical *Dynomene*, with *D. hispida*) have acquired a sternal structure (apomorphy). Despite the links Dromiidae/Dynomenidae within the Dromioidea, advanced dynomenids display an innovation with regard to dromiids in which the structures always depend on limbs. In these dynomenids the pair of sternal differentiations is positioned on thoracic somite 5 (more precisely on episternite 5) just facing the large dorsal uropods. In dynomenids, neither abdomen nor uropods are modified (whereas in dromiids the abdominal or uropodal border is ventrally or laterally modified). Modification of coxal structures into sternal structures is a consequence of the significant broadening of thoracic sternum (Figs 6, 7). These coxal or sternal structures are similar in their morphology and connection with abdomen (in overhanging, touching or lying quite apart from the abdominal margin) and play the same role in restricting its lateral movement at the very most. The dynomenid sternal structure has the same location, on sternite 5, as the button in the typical press-button of the Eubrachyura, but the involvement of the abdomen appears as quite different. In dynomenids it is not a press-button system: the abdomen is only loosely applied on the sternum and is only restricted in its sideways movements. An essential point is that the abdominal part (uropod included) is never modified in the dynomenid configuration. Such a combination is not inconsistent with the idea that sockets (in Homoloidea and Eubrachyura) are issued from uropods.

In brief, within the Brachyura a sternal structure has appeared:

– Once in Dynomenidae (sternite 5), without sockets.

– Once for all the Homoloidea (sternite 4): the homolid press-button is practically similar in the three families (Homolidae, Latreilliidae, Poupiniidae) and exhibits microstructures. The pair of sockets hollowed on abdominal segment 6 shows a configuration similar to sockets of the typical press-button in the Heterotremata-Thoracotremata assemblage.

– Once in the Raninoidea, but in a single subfamily, the Lyreidinae (sternite 5), with sockets. The concerned somite is the same as in dynomenids and in the Heterotremata-Thoracotremata assemblage. Locking is very efficient, even in females with eggs.

– Twice in the Cyclodorippoidea (sternite 6), probably separately in the Phyllotymolinidae and in the Cyclodorippidae. But no corresponding sockets exist, the telson being involved in locking by its movements along the sternal structures. Locking is very efficient.

– Once in the Eubrachyura (sternite 5), with sockets.

Two synapomorphies for the Heterotremata-Thoracotremata assemblage are: presence of a sterno-abdominal cavity, with delimited borders (present, however, in Cyclodorippoidea and in Dakoticancroidea), but not evolved in the most primitive families; presence of a press-button, which is typical and remains practically unchanged in all eubrachyuran crabs.

The novelty with a sternal differentiation has appeared independently several times within the Brachyura: five times in the Podotremata, and only once in the Heterotremata-Thoracotremata assemblage. The question of a common origin for both Lyreidinae and Eubrachyura needs further consideration.

Within the Brachyura a socket has appeared three times: in Homoloidea, Lyreidinae and Eubrachyura. Again, the question of a common origin for both Lyreidinae and Eubrachyura is highlighted. The condition in Eubrachyura, with a typical press-button on sternite 5, is not regarded as having evolved from a primitive stage as in dynomenids or homoloids for example.

The abdominal retaining mechanism used as paleontological data

The nature of fossil material does not preclude observation of the abdominal retaining/locking systems. When the coxae of pereiopods and anterior sternal plate are preserved, it could be easy to see if any process overhangs the telson and how the uropods (if present) may be involved. It can be deduced whether we are dealing with a podotrematous crab or not, and also to decide whether it is a homolodromiid instead of a homolid.

Projections arising from sternite 5 are present in several raninid fossils, for example in the Lyreidinae (*Lyreidus succedanus*, *L. rosenkrantzi*, *L. bispinulatus*, and *Rogeus orri*), but information is lacking on structures that might allow locking with sockets on pleomere 6, such as the hooks in the extant *Lyreidus* and *Lysirude*. A careful comparison with representatives of the exclusively fossil subfamily Palaeocorystinae, for example *Notopocorystes stokesii* (Mantell, 1844), is necessary.

In the case of an apparatus of the press-button type, the two parts are normally not visible when the abdomen is folded. But, in published illustrations, apparent sternal buttons can be clearly observed when the abdomen is lost or displaced. In *Ophthalmoplax stephensoni* Rathbun, 1935 (pl. 13, fig. 14), indicated as a female, two tubercles on sternite 5 seem to correspond to the buttons.

Male specimens of *Xanthopsis dufourii* (H. Milne Edwards, 1850) and *Harpactocarcinus souverbiei* A. Milne Edwards 1862, *Lobocarcinus paulinowurtembergensis* von Meyer, 1847, all three from the Lutetian, that were examined, have visible sternal prominences (Bouchard 1996, pl. 6, fig. 3a-c).

Fossil representatives of the family Retroplumidae, for example *Costaplumа concava*, *C. salamanca*, and *C. nordestina* which have their ventral surface preserved, show marked lateral expansions on pleomere 6 and a notch on sternite 4, thus a mechanism similar to that of extant species and probably efficient indeed.

Fossil leucosiids clearly exhibit the special features of their abdomen, fused with the sternal parts (Rathbun 1926, pl. 11). Morris & Collins (1991, figs 17b, 18, 24b) have shown Neogene leucosiids in which the spur on sternite 5 is clearly visible in a *Leucosia* species, but absent in two *Iphiculus* species.

The special structures shown by fossil brachyuran crabs deserve to be extensively studied.

Hypothesis about the homology uropod-socket

For Hessler (1983: 157, fig. 6) evolution of the eumalacostracan (caridoid) abdomen from that of a phyllocarid through fusion of the seventh original abdominal segment to the sixth occurred in concert with the evolution of the tail fan. He suggested that the sixth pleopods have evolved into uropods because they were the most posterior appendages. Uropods combined with telson to form the tail fan are present throughout the Decapoda [for other crustacean groups see Schram (1974) and Wilson (1996). Exceptions are the Lithodidae (uropods lost in males and females) and the Lomoidea (uropods reduced in females, lost in males) (Balss 1940; McLaughlin 1983a, b; Gruner 1993); all of these have essentially a flexed abdomen. There is obviously a functional significance to loss of uropods..

It is generally said that the uropods are lost in all Brachyura, except in the Dromiacea where they remain as vestiges. In establishing the new taxon Meiura (= reduced tail) to include the two monophyletic groups Anomura and Brachyura, Scholz & Richter (1995) have not stressed the important difference regarding the biramous uropods, present in (almost) all Anomura and always absent in Brachyura. Thus the character furnished by uropods in the most primitive crabs takes on great importance, and their role in abdominal retention deserves consideration. We attempt to demonstrate here that the socket hollowed on the sixth abdominal segment in brachyuran crabs is directly derived from the uropod.

Pérez (1928b: 649; 1929: 1145) has noted the resemblance between pagurids, which grasp and hold on to the shell's columella with their developed uropods, and dromiids which hold their abdomen with their vestigial dorsal uropods. He pointed out that the condition of *Dromia* may be a stage in evolution of the higher brachyuran condition. He concluded that in higher crabs the socket which allows fastening is perhaps "*le dernier vestige de l'uropode évanoui*" (last vestige of the disappearing uropod). Hartnoll (1975: 16), Guinot (1979a: 156) and Guinot & Richer de Forges (1997: 472) adopted the idea of a homology between the uropod and the socket. Even if the socket may be regarded as homologous with the uropod, we do not think that it is directly evolved from the dromiid dorsal uropod.

This homology is supported by several arguments:

– All the Podotremata which have vestigial uro-

TABLE 3. — Uropod patterns in Brachyura (in comparison to the biramous uropods in other Decapoda).

Taxon	Uropod pattern
PODOTREMATA	
Homolodromiidae	ventral lobes
Dynomenidae	dorsal plates
Dromiidae	dorsal plates
Exceptions:	
- *Hypoconcha*	ventral lobes
- *Exodromidia*	ventral lobes
- *Pseudodromia*	ventral lobes
- *Ascidiophilus*	absent
Homolidae	sockets
Latreilliidae	sockets
Poupiniidae	sockets
Cynomonidae	absent
Cyclodorippidae	absent
Phyllotymolinidae	absent
Raninidae	absent
Exception :	
Lyreidinae	sockets
HETEROTREMATA (*)	sockets
Exceptions:	
Corystidae	absent
Orithyidae	absent
Cryptochiridae	absent
Leucosiidae	absent
THORACOTREMATA	sockets
Exceptions:	
Grapsidae Sesarminae (*pro parte*)	absent
Grapsidae Varuninae (*pro parte*)	absent
Gecarcinidae (*pro parte*)	absent
Ocypodidae (*pro parte*)	absent
Mictyridae	absent

* Note that certain genera in the family Hymenosomatidae have dorsal platelets ventrally hollowed in deep sockets.

pods (dorsal plates or ventral lobes) are devoid of sockets (Dromiidae, Dynomenidae, Homolodromiidae), *i.e.* the Dromiacea.

– All the Homoloidea, which have no trace of appendagelike or dorsal or lobiform uropods, possess sockets (homolid press-button), as well in the primitive family Poupiniidae as in the most advanced one, the Latreilliidae.

– All (or nearly all) brachyuran crabs that always lack uropods possess sockets. Among the 57 families reviewed here the press-button characterizes 46 families.

– Examples of brachyuran crabs devoid of both uropods and sockets are very rare: the Raninidae (Lyreidinae excepted) and the Cyclodorippoidea (Table 3).

– Dorsal uropods, even when utilized in dromiids for abdominal retention, never bear a socket ventrally: they operate as a full-lock system and not as a press-button.

As previously said, it is accepted that the dorsal plates seen in the great majority of dromiids and in all dynomenids represent modified uropods. The transformation uropod-socket has necessarily required a substantial modification.

Ventral lobes of homolodromiids (and some dromiids) (see Table 3) obviously appear as rudiments of the appendages of pleomere 6, without a modification as important as in the case of dorsal uropods. The lobes resemble rudimentary pleopods found on preceding pleomeres in all *Homolodromia* and most of the *Dicranodromia* species (Guinot 1995: 179, figs 5, 25), but they differ by their insertion and orientation. Uropodal lobes, either with two articles or weakly bifid, were observed in certain homolodromiid species (*ibid.*). An argument to support that these ventral lobes are vestiges of the sixth pair of appendages is shown by their configuration in the Dynomenidae. In dynomenids, which have large dorsal uropodal plates (visible ventrally and dorsally, and larger than in dromiids), vestigial pleopods are always present on segments 3-5 in males. One could expect that, similarly, pleomere 6 might bear a ventral pair of pleopods 6: in fact, this site is occupied by the triangular uropod, the ventral surface of which is not hollowed (Figs 6B-D, 7C, D). It is our considered opinion that the dromioid dorsal uropods are specialized structures.

When, in the Brachyura, a socket was present on the sixth segment, no vestigial appendage has ever been observed on the third through fifth abdominal segments.

Case of the Hymenosomatidae

Within the Heterotremata, the Hymenosomatidae are particularly interesting because in the most primitive members of the family, the sockets are situated on intercalary platelets. What is more interesting is that the platelets may be movable, for example in the genera *Odiomaris* Ng

et Richer de Forges, 1996, *Amarinus* Lucas, 1980, and *Hymenosoma* Desmarest, 1825, *pro parte* (Guinot & Richer de Forges 1997).

Internal surface of the platelet is hollowed as a deep socket, externally bordered by a thickened calcified margin and separated from the pleotelson by a membrane (Bouchard 1996). These structures are clearly visible for example in *Odiomaris pilosus* (A. Milne Edwards, 1873) (better known as *Elamena pilosa* or *Amarinus pilosus*) (Fig. 27). In establishing *Amarinus angelicus*, Holthuis (1968: 115) described "a small movable segment attached to the base of the telson and the postero-lateral angle of the sixth somite" and

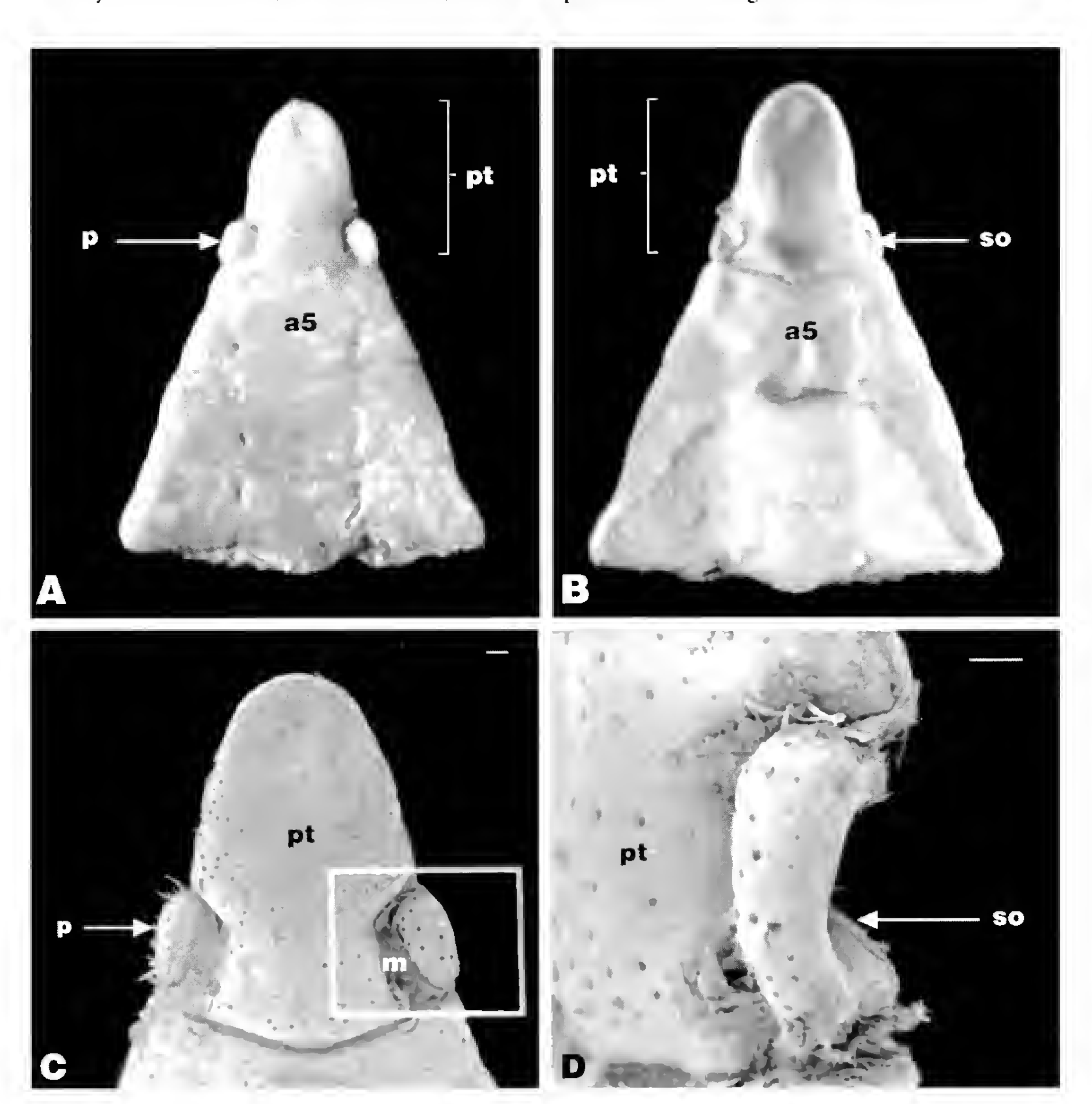


FIG. 27 — Locking apparatus in Hymenosomatidae, for example in *Odiomaris pilosus* (A. Milne Edwards), ♂ 20 × 22.6 mm, New Caledonia (MNHN-B 26146); **A**, **B**, abdomen in dorsal and ventral views; **C**, dorsal view of pleotelson; **D**, side view of the mobile intercalated platelet, with socket (**C**, **D**, scanning electron microscope photographs). Abbreviations: **a5**, abdominal segment 5; **m**, membranous zone; **p**, intercalated platelet; **pt**, pleotelson; **so**, socket. Scale bars: C, 200 µm; D, 100 µm.

remarked: "Such intercalated plates to my knowledge have so far not been reported from any brachyuran other than Dromiidae. Whether these structures in the present species and in the next [= *O. pilosus*] are homologous with those of the Dromiids, I am unable to say."

In fact, the Hymenosomatidae show several patterns: platelets movable; platelets simple and no longer articulated, with more or less distinct sutures (plesiomorphic condition); differentiations dorsally visible at the pleotelson base (for example the trilobate pleotelson in the genus *Hymenicoides* Kemp, 1917); prominences more or less marked. When the platelets disappear dorsally, the sockets are situated at the same place, wihout a visible external indication (apomorphic condition). All these pieces, either platelets or sockets, play the same role in covering the acute buttons of the press-button apparatus and firmly attaching the abdomen.

We will examine whether the morphological criteria provided here are sufficient for identifying uropods and sockets as homologues (Hennig 1966; Wiley 1981; Wägele 1996). The similarity of position (topographic and position in relation to other parts) is obvious. The socket is a more or less deep depression on abdominal somite 6, delimited by a calcified margin; the most thickened part of this margin is always latero-posterior, allowing an efficient locking with the button. In Eubrachyura (*Amarinus* and *Odiomaris* excepted) the socket is integrated into pleomere 6 and presents various forms: from rounded (Fig. 26B) to more or less elongated (Fig. 26D). In dorsal view, the movable hymenosomatid platelet significantly recalls a dorsal uropod, but its internal surface is hollowed as a deep socket. Thus, the hymenosomatid platelet ventrally looks like (and functions as) a socket; dorsally, it looks like a dorsal plate.

In researching the criterion of special similarity between uropods and sockets, one needs to investigate similarities of structure, for example in histological detail, and ontogenetic resemblance.

The criterion of phylogenetic position may reinforce homologues. Ventral lobes of homolodromiids might probably be considered as transitional passage between the decapod uropods and the sockets. In dromiids the uropods are often used to retain the abdomen. Ventral lobes are present in some primitive dromiids and do not play any role. The movable and articulated dorsal uropods of certain dromiid forms are apparently more primitive that the fused ones. The large and always completely dorsal plates in dynomenids, that are more advanced, appear as derived. We remark that in the brachyuran evolutionary scheme, where uropods are lost, sockets are uniformly developed in the same location, on abdominal somite 6. As already remarked, the trends toward loss of abdominal limbs are components of the carcinization process in the Decapoda. The novelty represented by the socket may be regarded as the character state presence of uropod, but we ignore the process of differentiation from the uropod into the socket.

The Brachyura which possess lobe-shaped ventral uropods or plate-shaped dorsal uropods, are recognized as being more primitive (dromiids, dynomenids) than those having sockets at the same location (Homoloidea, Lyredinae, and Eubrachyura).

The critetion of position is provided by a strict and constant location of ventral lobes, dorsal plates, platelets, and sockets on pleomere 6. Even in the cases where the sockets appear atypically positioned, they belong to the same pleomere. For example, when sockets are found on the last element of abdomen (Hymenosomatidae Fig. 27, Inachoidinae Fig. 20C-F, and in a part of the Inachinae Fig. 20A, B), this is easily explained by the fusion as pleotelson of segment 6 with telson.

The criterion of continuance through intermediate forms may be provided by presence of movable dorsal uropods in dromiids and movable platelets in hymenosomatids. Dromiid uropods, that are never used when applied on a surface but act in full-lock, lack ventral sockets, while the hymenosomatid platelets are ventrally hollowed and operate as a press-button. Absence of sockets in advanced Brachyura (*pro parte* Grapsidae, Gecarcinidae, Ocypodidae) is considered to be the result of a secondary loss.

In conclusion the appendages of the sixth abdominal segment are practically always present in Decapoda, but with different patterns (biramous limb, rasp, lobe, plate, platelet, socket). Hence it is probably not accurate to define the Brachyura by the absence of uropods.

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The types of Recent and certain fossil opisthobranch molluscs in the Muséum national d'Histoire naturelle, Paris

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ABSTRACT
Three hundred and fifty seven lots of Recent and certain fossil opisthobranch mollusc type-specimens deposited in the Laboratoire des Invertébrés Marins et Malacogie of the Muséum national d'Histoire naturelle (MNHN) are catalogued by original binomen and arranged alphabetically within families. Most of the fossil type specimens are housed in the Laboratoire de Paléontologie, and therefore are not included in this catalogue. The essential bibliographical, geographical and taxonomic information is provided for each taxon.

KEY WORDS
type specimens,
opisthobranchs,
Mollusca,
MNHN, Paris.

RÉSUMÉ
Les types actuels et de quelques fossiles de mollusques opisthobranches du Muséum national d'Histoire naturelle, Paris. Trois cent cinquante-sept types d'opisthobranches actuels et quelques fossiles déposés au Laboratoire de Biologie des Invertébrés Marins et Malacologie du Muséum national d'Histoire naturelle (MNHN) ont été identifiés et listés par ordre alphabétique d'espèces à l'intérieur de chaque famille. La plupart des types fossiles se trouvent au Laboratoire de Paléontologie et ne sont pas mentionnés dans cette liste. Les principales références bibliographiques, géographiques et taxonomiques accompagnent chaque porte-nom.

MOTS CLÉS
types,
opisthobranches,
Mollusca,
MNHN, Paris.

INTRODUCTION

In recent years, opisthobranch systematists have become increasingly interested in examining type material as part of their research. However, the scarcity of updated museum opisthobranch type catalogues make this task arduous and time consuming. Most museum opisthobranch type collections consist of historically important specimens for which the identification of type specimens, and the determination of their status, is usually difficult to resolve with certainty. Often, old type specimens remain unrecognized in the general collections, which may house types of species not expected to be present at that museum.

The objective of this paper is to document the present collection and scope of the Recent and certain fossil opisthobranch name-bearing type specimens in the Muséum national d'Histoire naturelle of Paris (MNHN). This will facilitate future systematic research based on this material.

A BRIEF HISTORY OF THE COLLECTIONS

The Muséum national d'Histoire naturelle in Paris (MNHN) was founded in 1793, and shortly thereafter, the first opisthobranch type specimens were deposited in its collections. The earliest major collections extant are those of the French expeditions to exotic countries, carried out during the early nineteenth century (l'*Astrolabe*, l'*Uranie*, Savigny expedition to Egypt, d'Orbigny expedition to South America, Péron expeditions to the Indo-Pacific), described by the French classic authors: G. Cuvier, J. C. Quoy & J. P. Gaimard, J. V. Audouin, A. de Férussac, P. S. Rang, A. d'Orbigny, L. F. A. Soulcyet.

In the second half of the nineteenth century, and the beginning of the twentieth century, the French carried out a significant collecting effort in their colonies in the Caribbean, Africa, Eastern Asia and South-West Pacific. This material, added to MNHN collections, was also mainly described by French authors (G. Deshayes, L. Morlet, A. T. de Rochebrune, P. Fischer). At about the same time, L. Morlet and H. Crosse described several opisthobranch fossil species whose types are now in MNHN, and new oceanographic expeditions (*Cap Horn*, *Travailleur* et *Talisman*, *Diguet* expedition to Baja California, French Antarctic expeditions, Gravier Expedition to Djibouti) were an additional source of type specimens, mostly described by A. Locard, P. Fischer, J. B. M. Vayssière and J. Risbec.

During the First and Second World Wars, unlike several natural history museums in Europe, the MNHN collections remained untouched. In these and in the following years, many type specimens were added as a result of the work of A. Pruvot-Fol who described material collected abroad and from the French coasts. However the types of many species that she described could never be found, possibly because the specimens were discarded after dissection; the extant material is mostly that of formal expeditions or museum holdings that were entrusted to her for description. Material from the *Calypso* expeditions was also described by Ev. Marcus. In the late 1950s, the Fischer family shared the property of *Journal de Conchyliologie*. E. Fischer-Piette, then professor and director of the Laboratoire de Malacologie, donated the type collection of the *Journal*, containing a number of opisthobranch types. At that time, the Muséum wet collections were stored in high glass containers, at the Galerie de Zoologie, the main exhibit building. When this gallery was closed to the public in 1965 the collections remained there, and many specimens went dry, or were otherwise damaged.

A new age in the MNHN opisthobranch collection, characterized by the internationalization of the scope of the type collection, started with the arrival of P. Bouchet on the staff in 1975. He not only added his own types, but also was instrumental in encouraging authors from other countries to deposit their type specimens in MNHN. Many significant types of European and African species were contributed through the Spanish school (J. A. Ortea, J. C. García-Gómez, and others), and Indo-Pacific material collected by French scientists were described by W. B. Rudman (some of them still on extended loan).

In 1985, the MNHN scientific collections were moved to a new, large underground storage building, and the type specimens of Recent and certain fossil molluscs were separated and placed in

a repository in the Laboratoire de Biologie des Invertébrés Marins et Malacologie. However, the opisthobranch collection still remained in need of curation for several years. The older type specimens were stored together with other material in antiquated fashion, and no longer suitable containers, and it was difficult to find specific lots. In fact, there are some examples in the recent literature of type specimens considered lost (Wägele 1985, 1990) that have recently appeared. For this reason, the first author of this paper was kindly invited in 1995 to work at MNHN as an assistant curator, to reorganize the opisthobranch collection, and separate the type specimens. This task, carried out in collaboration with the second author, was concluded during another short-term stay in 1997, with the final separation and inventory of all type specimens. During this work, we have also found several types of species described by authors whose type material was not expected to be in MNHN. Some of them are replacement names, names introduced under the Article 70c (ICZN 1985), or specimens apparently borrowed by A. Vayssière from other institutions, never returned and later deposited at MNHN.

Type Catalogue

The catalogue of Recent and certain fossil types of opisthobranch molluscs in MNHN covers three hundred and fifty-three lots of name-bearing type specimens. However, it does not include most of the fossil species in MNHN which are stored in the Laboratoire de Paléontologie (*e.g.* the Cossmann collection).

This catalogue is restricted to name-bearing types: holotypes, lectotypes, neotypes and syntypes. Other type lots (paratypes and paralectotypes) are in (or will be transferred to) the general collection, and are only included in the catalogue as accessory material of the name-bearing types. All type specimens are listed by species-group names and arranged alphabetically within families. To facilite the search, the complete list of names, arranged alphabetically, indicating the family, higher category taxa and page number where each name has been placed is included. When the same lot is the type of two different species-group names, they are listed separately, unless if they are identically spelled. The essential taxonomic, geographical and bibliographical information is provided for each species-group name. These data include the name of the species cited exactly as published in the original description, the author, date and bibliographic reference, the type locality as originally printed and its modern geographical equivalent, the category and number of specimens, state of conservation, accessory material (*e.g.* photographs, microscopy slides, spawn or food of the specimens, paratypes and paralectotypes), and the name of the collector when it is known. The old geographic names, no longer used, are printed between quotation marks. The names of large geographic areas, countries or archipelagos are translated into English, but other names are printed in their local spelling. The state of conservation includes two main items: "specimen", which refers to specimens conserved in alcohol complete of soft parts, and "shell", when only a shell remain in the dry collection. When the type specimen held is also known to be originally or subsequently figured it is indicated. All shells (with the exception of four nominal species catalogued while the paper was already in press) are illustrated, even if they have been previously figured. Figured specimens are individually identified in the collection. Short remarks with the currently accepted taxonomic status of the species, lectotype designations, status as type species of genus-group names, or any other useful information are given. No attempt has been made to list the synonyms of each species, but opinions on the taxonomic status of several names have been included (only when they are based in the examination of the type material or are derived from an exhaustive revision). All names have been grouped in families on the basis of available literature. When it was not possible we have been obliged to adopt our own view, which obviously requires confirmation by further studies. This is not a critical review of the material, but merely is an attempt to make its usage easier.

The families are enumerated in the order of the classification followed by Rudman & Willan (1998), with nomenclatural adjustments (Bouchet & Rocroi, pers. comm.).

CEPHALASPIDEA

Family ACTEONIDAE d'Orbigny, 1842

azoricus. *Actaeon azoricus* Locard, 1897: 85-87, pl. 3, figs 8-11. Type locality: *Talisman* (1883) Expedition, stn 126, 38°37'N - 28°21'W, between Pico and S. Jorge, Azores, 1258 m. HOLOTYPE (by monotypy, figured by Locard, 1897, pl. 3, figs 8-11): shell (Fig. 1A). **Remarks**: This is the type species of the genus *Inopinodon* Bouchet, 1975, by original designation.

maltzani. *Actaeon maltzani* Dautzenberg, 1910: 10, pl. 1, figs 1, 2. Type locality: Baie de Rufisque and Gorée, Senegal. SYNTYPE (figured by Dautzenberg, 1910: pl. 1, figs 1, 2): 1 shell (Fig. 1B). **Remarks**: Dautzenberg (1910) placed *Tornatella senegalensis* Petit de la Saussaye, 1851 in the genus *Acteon* de Montfort, 1810 (cited as *Actaeon*) and therefore *Actaeon senegalensis* Maltzan, 1885 becomes a junior secondary homonym of *A. senegalensis* (Petit de la Saussaye, 1851). Therefore, Dautzenberg (1910) introduced the replacement name *Actaeon maltzani* for it. This new species was based on Maltzan's material and newly collected specimens studied by Dautzenberg. All of them are syntypes of this species.

morelletorum. *Actaeon morelletorum* Gougerot *et* Braillon, 1968: 200, pl. 1, fig. 3. Type locality: Barisseuse, France (middle Eocene). HOLOTYPE (by original designation, figured by Gougerot & Braillon pl. 1, fig. 3).

vagabunda. *Tornatella vagabunda* Mabille, 1885: 208. Type locality: Magallanes, Chile. SYNTYPE: 1 shell (Fig. 1C).

Family APLUSTRIDAE Gray, 1847
[= HYDATINIDAE Pilsbry, 1895]

eximia. *Bulla eximia* Deshayes, 1863: 55, 56, pl. 7, figs 23, 24. Type locality: La Réunion (Indian Ocean). SYNTYPES: 3 shells (Fig. 1D).

guamensis. *Bullaea guamensis* Quoy *et* Gaimard, 1824: 423-425, pl. 66, figs 10-12. Type locality: Agana, Guam (Pacific Ocean). SYNTYPE: 1 specimen, leg. Quoy and Gaimard. **Remarks**: Pruvot-Fol (1934b) placed this species in the genus *Micromelo* Pilsbry, 1894.

Family RINGICULIDAE Philippi, 1853

admirabilis. *Ringicula admirabilis* Morlet, 1883: 203, 204, pl. 9, fig. 3. Type locality: Mediterranean Sea. SYNTYPE: 1 shell, leg. Morlet (Fig. 1E). **Remarks**: This is the type species of the genus *Plicatra* Nordsieck, 1972, by original designation. According to Ciccone & Savona (1982), this species is a junior synonym of *Ringicula conformis* Monterosato, 1877.

bourgeoisi. *Ringicula bourgeoisi* Morlet, 1878b: 261, 262, pl. 8, fig. 5. Type locality: Pontlevoy, Paulmy, Ferrières l'Arçon, Manthelan (France, middle Miocene), Mandillot (France, early Miocene). SYNTYPES: 3 shells, leg. Crosse (Fig. 1F).

bourguignati. *Ringicula bourguignati* de Rochebrune, 1883: 178. Type locality: Casamance, Senegal. SYNTYPES: 2 shells (Fig. 1G).

caledonica. *Ringicula caledonica* Morlet, 1880: 154, 155, pl. 5, fig. 1. Type locality: "Plage de la Baie Pouen" (= Baie de Pritzbuer), New Caledonia. SYNTYPES: 14 shells, leg. Morlet (Fig. 1H).

crossei. *Ringicula crossei* Morlet, 1878b: 273, 274, pl. 7, fig. 11. Type locality: various localities in central and western Europe (middle and upper Miocene). SYNTYPE: 1 shell, leg. Crosse (Fig. 1I).

gaudryana. *Ringicula gaudryana* Morlet, 1878b: 283, 284, pl. 7, fig. 12. Type locality: various localities in central and western Europe (middle Miocene to Pliocene). SYNTYPE: 1 shell, leg. Crosse (Fig. 1J).

mariei. *Ringicula mariei* Morlet, 1880: 152, 153. Type locality: "Nossibé" (= Nosy Be), Madagascar. SYNTYPES: 9 shells, leg. de Folin (Fig. 2A).

minutula. *Ringicula minutula* Locard, 1897: 89, 90, pl. 14, figs 7-9. Type locality: *Talisman* (1883) Expedition, stn 84, 22°54'N - 17°26'W, off Sahara, 860 m. SYNTYPE: 1 shell (Fig. 2B).

noumeensis. *Ringicula noumeensis* Morlet, 1880: 155, 156, pl. 5, fig. 3. Type locality: Nouméa, New Caledonia. SYNTYPES: 18 shells, leg. Morlet (Fig. 2C).

oehlertiae. *Ringicula oehlertiae* Morlet, 1880:

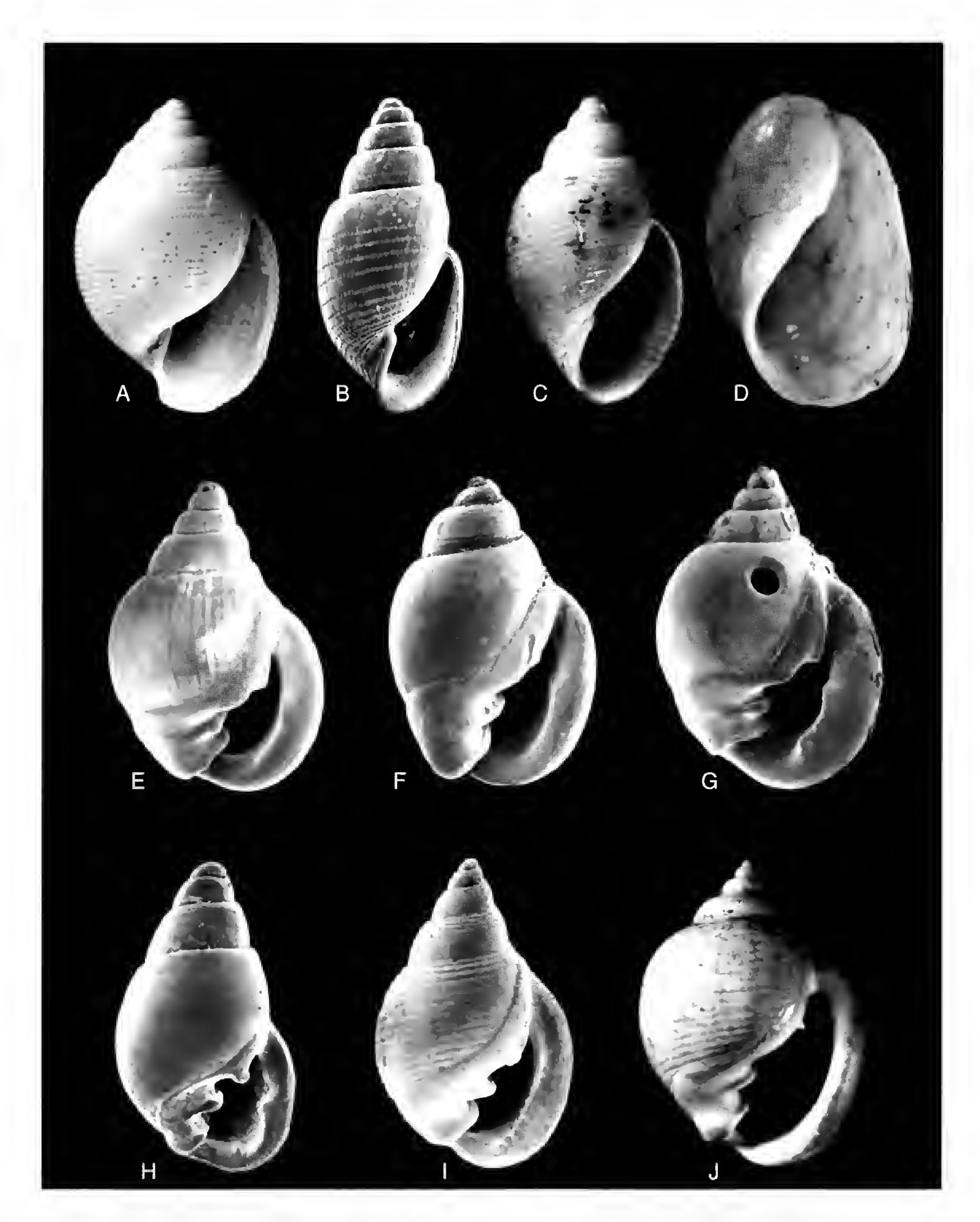


FIG. 1. — **A**, holotype of *Actaeon azoricus*, 11.3 mm; **B**, syntype of *Actaeon maltzani*, 3.1 mm; **C**, syntype of *Tornatella vagabunda*, 8.2 mm; **D**, syntype of *Bulla eximia*, 10.2 mm; **E**, syntype of *Ringicula admirabilis*, 3.6 mm; **F**, syntype of *Ringicula bourgeoisi*, 3.9 mm; **G**, syntype of *Ringicula bourguignati*, 4.0 mm; **H**, syntype of *Ringicula caledonica*, 1.9 mm; **I**, syntype of *Ringicula crossei*, 3.7 mm; **J**, syntype of *Ringicula gaudryana*, 7.2 mm.

156, 157, pl. 5, fig. 4. Type locality: Seas of China and Japan. SYNTYPES: 3 shells, leg. Morlet and Saint-John (Fig. 2D).

passieri. *Ringicula passieri* Morlet, 1880: 157, 158, pl. 5, fig. 5. Type locality: Cap Breton Canyon, Bay of Biscay. SYNTYPE: 1 shell, leg. de Folin (Fig. 2E).

paulucciae. *Ringicula paulucciae* Morlet, 1878b: 266, 267, pl. 6, fig. 6, pl. 8, fig. 9. Type locality: Saucats and Dax, France (early Miocene). SYNTYPE: 1 shell, leg. Crosse (Fig. 2F).

pirulina. *Ringicula pirulina* Locard, 1897: 87, 88, pl. 14, figs 1-6. Type locality: *Talisman* (1883) Expedition, stn 33, 32°31'N - 09°48'W, off Atlantic coast of Morocco, 1350 m. SYNTYPES: 2 shells (Fig. 2G). **Remarks**: According to Bouchet (1975b), this is a junior synonym of *Ringicula nitida* Verrill, 1874.

ponteleviensis. *Ringicula ponteleviensis* Morlet, 1878b: 274, 275, pl. 8, fig. 8. Type locality: various localities in France (middle Miocene). SYNTYPE: 1 shell, leg. Crosse (Fig. 2H).

pulchella. *Ringicula pulchella* Morlet [*ex* Jeffreys MS], 1880: 158, pl. 5, fig. 6. Type locality: Atlantic European. SYNTYPES: 4 shells (Fig. 2I). **Remarks**: This is the type species of the subgenus *Ringactaeon* Nordsieck (1972) by original designation.

quadriplicata. *Ringicula quadriplicata* Morlet, 1878b: 286, 287, pl. 7, fig. 1. Type locality: several localities in Europe (middle and upper Miocene, and lower Pliocene). SYNTYPE: 1 shell, leg. Crosse (Fig. 3A).

rosildae. *Ringicula rosildae* Rosso *et* Saubade, 1985: 305, 306, figs 8-11. Type locality: 14°36'30"N - 17°15'30"W, off Senegal. HOLOTYPE: said to be deposited in MNHN in the original publication, but never presented to the museum.

roussellae. *Ringicula roussellae* Rosso *et* Saubade, 1985: 303, 304, fig. 2. Type locality: 14°22'40"N - 17°09'W, off Senegal. HOLOTYPE: said to be deposited in MNHN in the original publication, but never presented to the museum.

salleana. *Ringicula salleana* Morlet, 1880: 153, 154. Type locality: Cap Breton Canyon, Bay of Biscay. SYNTYPE (probably): 1 shell, leg. de Folin (Fig. 3B).

savignyi. *Ringicula savignyi* Morlet, 1878a: 117, 118, pl. 5, fig. 1. Type locality: Suez, Egypt (Red Sea). SYNTYPES (one figured by Bouchet & Danrigal 1982, fig. 59): 10 shells, leg. Savigny (Fig. 3C).

schlumbergeri. *Ringicula schlumbergeri* Morlet, 1883: 204-206, pl. 9, fig. 4. Type locality: Mediterranean Sea. SYNTYPES: 3 shells, leg. Morlet (Fig. 3D). **Remarks**: According to Ciccone & Savona (1982), this is a junior synonym of *Ringicula conformis* Monterosato, 1877.

senegalensis. *Ringicula senegalensis* Morlet, 1883: 202, 203, pl. 9, fig. 2. Type locality: Senegal. SYNTYPES: 2 shells, leg. de Folin (Fig. 3E).

terquemi. *Ringicula terquemi* Morlet, 1880: 159, 160, pl. 5, fig. 7. Type locality: "Baie de Smyrne" (= Bay of Izmir), Turkey. SYNTYPES: 5 shells, leg. Terquem (Fig. 3F). **Remarks**: According to Ciccone & Savona (1982), this is a junior synonym of *Ringicula auriculata* (Ménard de la Groye, 1811).

tournoueri. *Ringicula tournoueri* Morlet, 1878b: 287, 288, pl. 6, fig. 10. Type locality: various localities in central and western Europe (Neogene). SYNTYPE: 1 shell, leg. Crosse (Fig. 3G).

Family CYLICHNIDAE H. *et* A. Adams, 1854
[= TORNATINIDAE P. Fischer, 1883]

abyssicola. *Mamillocylichna abyssicola* Bouchet, 1975b: 349, 350, fig. 14. Type locality: *Biaçores* Expedition, stn 251, 47°38'N - 08°56'W, Banc de la Chapelle, 3360-3600 m. HOLOTYPE (by original designation): shell (Fig. 4F).

crossei. *Cylichna crossei* Bucquoy, Dautzenberg *et* Dollfus, 1886: 526, 527, pl. 64, figs 9-11. Type locality: not specified; cited from Canet, France, Viareggio, Italy and Alger. SYNTYPES (One figured by Bucquoy, Dautzenberg & Dollfus 1886: 526: pl. 64, fig. 9): 2 shells from Alger.

imperceptus. *Meloscaphander imperceptus* Bouchet, 1975b: 341-343, figs 9, 10, pl. 3, figs G-H. Type locality: *Talisman* (1883) Expedition, off Mauritania. HOLOTYPE (by original designation, figured by Bouchet,



FIG. 2. — **A**, syntype of *Ringicula mariei*, 1.7 mm; **B**, syntype of *Ringicula minutula*, 2.9 mm; **C**, syntype of *Ringicula noumeensis*, 3.7 mm; **D**, syntype of *Ringicula oehlertiae*, 3.9 mm; **E**, syntype of *Ringicula passieri*, 4.2 mm; **F**, syntype of *Ringicula paulucciae*, 3.4 mm; **G**, syntype of *Ringicula pirulina*, 6.8 mm; **H**, syntype of *Ringicula ponteleviensis*, 3.2 mm; **I**, syntype of *Ringicula pulchella*, 2.7 mm.

1975b, pl. 3, fig. H): shell (Fig. 4G) + 1 paratype.

insperata. *Bulla insperata* P. Fischer *in* Locard 1897: 54, 55, pl. 1, figs 19-22. Type locality: *Talisman* (1883) Expedition, stn 76, 25°01'N - 16°55'W, off Sahara, 2638 m. SYNTYPES: 2 specimens (1 of them dissected). **Remarks**: According to Bouchet (1975b), this is a junior subjective synonym of *Scaphander mundus* Watson, 1886.

lemchei. *Cylichna lemchei* Bouchet *et* Warén, 1979: 228, 229, figs 16, 18G, H, J-L. Type locality: *Norbi* Expedition, stn CP02 (64°26'-64°19'N, 01°36'-01°44'E) Norwegian Sea. HOLOTYPE (by original designation, figured by Bouchet & Warén 1979, fig. 18J-L): shell (Fig. 4H).

millepunctata. *Bulla millepunctata* Locard, 1897: 52-54, pl. 2, figs 3-6. Type locality: not specified; cited from *Talisman* (1883) Expedition, several stations, off Sahara, Senegal and Azores. SYNTYPES: 1 specimen and 2 shells (Fig. 4I). **Remarks**: This is the type species of the subgenus *Bullocardia* Nordsieck, 1972, by original designation. According to Bouchet (1975b), this is a junior subjective synonym of *Scaphander nobilis* Verrill, 1884.

mirabilis. *Tornatina mirabilis* Locard, 1897: 72, 73, pl. 2, figs 20-24. Type locality: *Travailleur* (1882) Expedition, stn 23, 38°21'N - 09°27'W, off Portugal, 2000 m. SYNTYPE: 1 shell (Fig. 5A).

morelletorum. *Cylichna morelletorum* Gougerot *et* Le Renard, 1983: 82, 85, fig. 12. Type locality: Ferme de l'Orme, France (middle Eocene). SYNTYPES: 24 shells.

olivaeformis. *Tornatina olivaeformis* Issel, 1869: 171, 172. Type locality: Gulf of Suez, Egypt (Red Sea). SYNTYPE (figured by Savigny 1817, pl. 6, fig. 25 and Bouchet & Danrigal 1982, fig. 56): 1 shell (Fig. 5E).

petiti. *Cylichna petiti* Dautzenberg, 1923: 70, 71, fig. text. Type locality: "Fénérive" (= Fenoarivo Atsinanana), Madagascar. HOLOTYPE (by monotypy, figured by Dautzenberg, 1923, fig. text): shell (Fig. 5B).

pusillina. *Tornatina pusillina* Locard, 1897: 75-77, pl. 2, figs 29, 30. Type locality: *Travailleur* (1880) Expedition, drag. 2, 43°46'N - 01°55'W, Cantabrian Sea, North of Spain, 1019 m. SYNTYPE: 1 shell (Fig. 5F).

scaphandroides. *Roxania scaphandroides* Staadt *in* Cossmann & Pissarro 1913, pl. 55, fig. 242-12. Type locality: Chenay, France (late Paleocene). HOLOTYPE (by monotypy, figured by Cossmann & Pissarro 1913, pl. 55, fig. 242-12): shell (Fig. 5C).

villersii. *Bulla villersii* Audouin, 1826: 39. Type locality: Egypt. SYNTYPES (one figured by Savigny, 1817, pl. 5, fig. 4 and Bouchet & Danrigal 1982, fig. 53): 2 shells (Fig. 5D).

voluta. *Bulla voluta* Quoy *et* Gaimard, 1833: 359, 360, pl. 26, figs 33-35. Type locality: Guam (Pacific Ocean). SYNTYPE: 1 shell, leg. Quoy and Gaimard (Fig. 5G). **Remarks**: Pruvot-Fol (1934b) placed this species in the genus *Acteocina* J. E. Gray, 1847.

Family RETUSIDAE Thiele, 1925

canariensis. *Cylichnina canariensis* Nordsieck *et* García-Talavera, 1979: 178, pl. 44, fig. 46. Type locality: Tenerife, Canary Islands. SYNTYPE: 1 shell (Fig. 5H).

candidula. *Cylichna candidula* Locard, 1892: 28. Type locality: Atlantic, coast of France. SYNTYPE: 1 shell (Fig. 5I).

desgenettii. *Bulla desgenettii* Audouin, 1826: 39. Type locality: Egypt. SYNTYPES (one figured by Savigny 1817, pl. 5, fig. 6 and Bouchet & Danrigal 1982, fig. 55): 5 shells (Fig. 5J).

dilatata. *Retusa dilatata* Pallary, 1904: 215, 216, pl. 7, fig. 8. Type locality: Gulf of Gabès, Tunisia. SYNTYPES: 11 shells (Fig. 5K). **Remarks**: Pallary (1904) selected a 6 mm long shell as the "type" of this species. However, in MNHN collection there are two vials with 4 and 7 shells respectively, all of them similar in length (about 6 mm), which therefore are considered syntypes.

fourierii. *Bulla fourierii* Audouin, 1826: 39. Type locality: Egypt. HOLOTYPE (by monotypy, figured by Savigny, 1817, pl. 5, fig. 5 and Bouchet & Danrigal 1982, fig. 54): shell (Fig. 5L).

girardi. *Bulla girardi* Audouin, 1826: 39. Type locality: Egypt. HOLOTYPE (by monotypy,

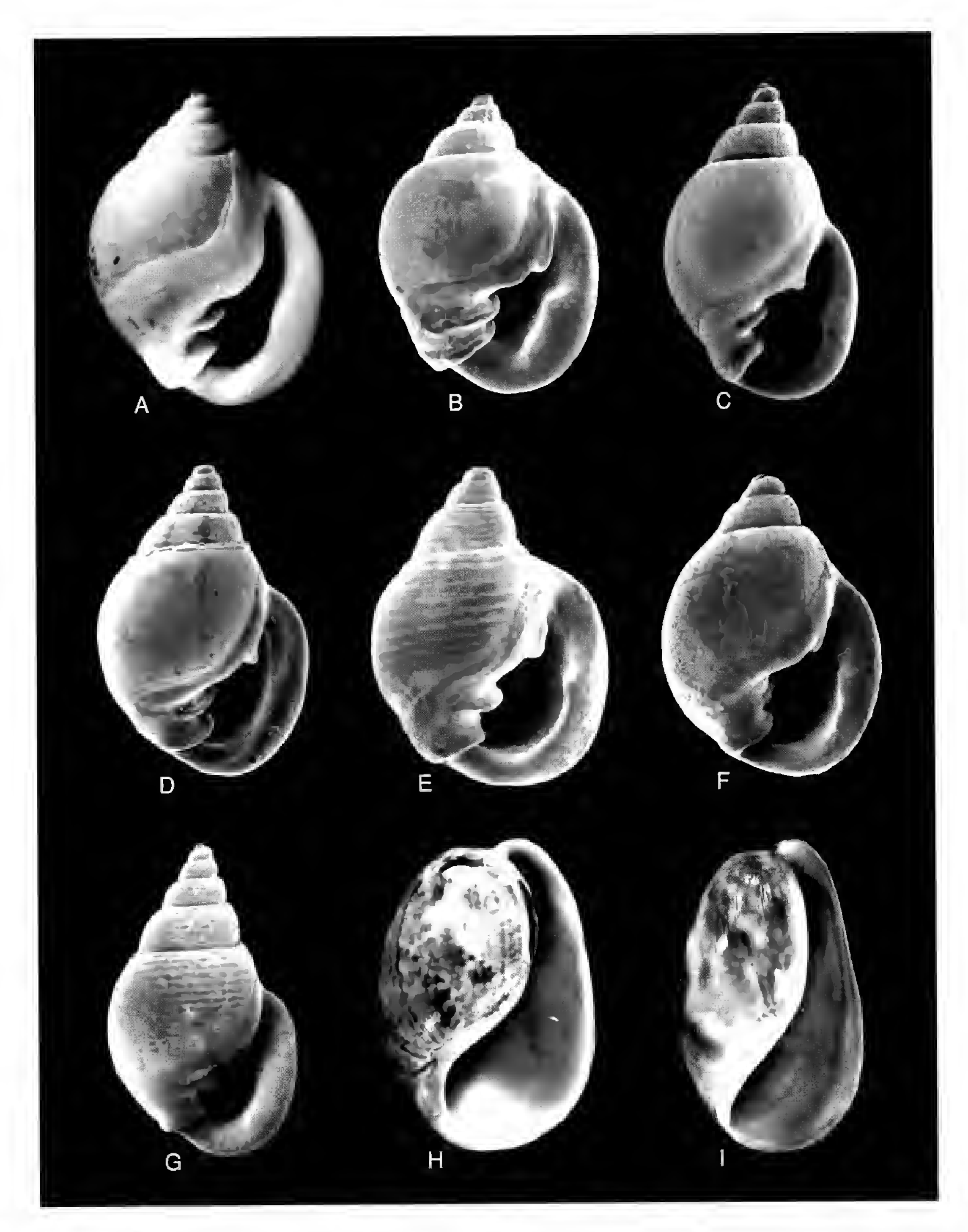


Fig. 3. — **A**, syntype of *Ringicula quadriplicata*, 8.9 mm; **B**, probable syntype of *Ringicula salleana*, 5.0 mm; **C**, syntype of *Ringicula savignyi*, 2.8 mm; **D**, syntype of *Ringicula schlumbergeri*, 3.1 mm; **E**, syntype of *Ringicula senegalensis*, 2.3 mm; **F**, syntype of *Ringicula terquemi*, 1.8 mm; **G**, syntype of *Ringicula tournoueri*, 4.3 mm; **H**, syntype of *Bulla australis* de Ferussac, 41.6 mm; **I**, syntype of *Bulla australis* Quoy et Gaimard, 49.4 mm.



FIG. 4. — **A**, holotype of *Bulla mongii*, 1.4 mm; **B**, syntype of *Bulla orbignyana*, 16.1 mm; **C**, syntype of *Bulla ovoidea*, 13.6 mm; **D**, syntype of *Haminea perrieri*, 16.4 mm; **E**, holotype of *Cylichnium waldae*, 28.1 mm; **F**, holotype of *Mamillocylichna abyssicola*, 2.8 mm; **G**, holotype of *Meloscaphander imperceptus*, 19.3 mm; **H**, holotype of *Cylichna lemchei*, 7.1 mm; **I**, syntype of *Bulla millepunctata*, 41.0 mm.



FIG. 5. — **A**, syntype of *Tornatina mirabilis*, 2.6 mm; **B**, holotype of *Cylichna petiti*, 6.5 mm; **C**, holotype of *Roxania scaphandroides*, 12.9 mm; **D**, syntype of *Bulla villersii*, 1.3 mm; **E**, syntype of *Tornatina olivaeformis*, 3.3 mm; **F**, syntype of *Tornatina pusillina*, 2.0 mm; **G**, syntype of *Bulla voluta*, 9.7 mm, **H**, syntype of *Cylichnina canariensis*, 2.6 mm; **I**, syntype of *Cylichna candidula*, 4.2 mm; **J**, syntype of *Bulla desgenettii*, 1.7 mm; **K**, syntype of *Retusa dilatata*, 5.7 mm; **L**, holotype of *Bulla fourierii*, 2.5 mm.

figured by Savigny 1817, pl. 5, fig. 3 and Bouchet & Danrigal 1982, fig. 52): shell (Fig. 6A). **Remarks**: This is the type species of the genus *Bullina* Risso *in* Audouin 1826, by monotypy.

simplex. *Bulla simplex* Locard, 1897: 55-57, pl. 2, figs 7-9. Type locality: *Talisman* (1883) Expedition, stn 75, 25°01'N - 16°53'W, off Sahara, 2325-2518 m. SYNTYPES: 8 shells (Fig. 6B). **Remarks**: Bouchet (1975b) transferred this species to the genus *Relichna* Rudman, 1971.

tenerifensis. *Cylichnina tenerifensis* Nordsieck *et* García-Talavera, 1979: 177, 178, pl. 44, fig. 45. Type locality: Tenerife, Canary Islands. SYNTYPE: 1 shell (Fig. 6C). **Remarks**: In the caption of the fig. 45 the name of this species is spelled *Cylichnina teneriffae*.

truncatella. *Cylichna truncatella* Locard, 1886: 533-534. Type locality: Cannes, France. SYNTYPES: 3 shells (Fig. 6D). **Remarks**: According to Lemche (1948), this is a junior subjective synonym of *Retusa truncatula* (Bruguière, 1792).

Family PHILINIDAE J. E. Gray, 1850

azorica. *Philine azorica* Bouchet, 1975b: 353, 354, fig. 17, pl. 4, figs F, I. Type locality: *Biaçores* Expedition, stn 167, 37°46'N - 25°48'W, off Azores, São Miguel, 140 m. HOLOTYPE (by original designation, figured by Bouchet 1975b, fig. 17, pl. 4, figs F, I): specimen (dried) + shell (Fig. 6E) and dried fragments.

milneedwardsi. *Philine milneedwardsi* Locard, 1897: 35-37, pl. 1, figs 7-9. Type locality: *Talisman* (1883) Expedition, stn 107, "Rade de Porte Grande" (= Porto Grande), São Vicente, Cape Verde Islands, 75-90 m. SYNTYPES: 2 shells (Fig. 6F).

monilifera. *Philine monilifera* Bouchet, 1975b: 354-356, fig. 18, pl. 4, figs D, E. Type locality: *Biaçores* Expedition, stn 41, 37°43'N - 29°04'W, off Azores, Princesse Alice Bank, 450-475 m. HOLOTYPE (by original designation): shell (Fig. 6G) + dried fragments.

Family AGLAJIDAE Pilsbry, 1895

hirundinina. *Bulla hirundinina* Quoy *et* Gaimard, 1833: 367-369, pl. 26, figs 20-25. Type locality: "Îlots aux Cerfs", "Île de France" (= Mauritius), Indian Ocean. SYNTYPES: 4 specimens (1 of them dissected), leg. Quoy and Gaimard. **Remarks**: This is the type species of the genus *Chelidonura* A. Adams, 1850, by monotypy.

quinza. *Aglaja quinza* Ev. Marcus, 1979: 132, 133, figs 1-4. Type locality: *Calypso* Expedition, stn 115, 23°56'S - 44°17'W, between Rio de Janeiro and Santos, Brazil, 23 m. HOLOTYPE (by monotypy, figured by Ev. Marcus 1979, figs 1-4): specimen (dissected) + shell and male organ slides.

seurati. *Doridium seurati* Vayssière, 1926: 125-128, pl. 13. Type locality: "près de la Skhirra" (= near Sakhira), Gulf of Gabès, Tunisia. SYNTYPES: 11 specimens. **Remarks**: Rudman (1972a) placed this species in the genus *Melanochlamys* Cheeseman, 1881.

Family HAMINEIDAE Pilsbry, 1925

africana. *Aceras africana* P. Fischer *in* Locard 1897: 62, 63, pl. 2, figs 15-19. Type locality: not specified; cited from *Talisman* (1883) Expedition, stn 96, 19°19'N - 18°02'W, off Mauritania, 2320-2333 m, and stn 101, 16°38'N - 18°24'W, Cape Verde Islands, 3200 m. SYNTYPE: 1 shell (Fig. 7E) from stn 96. **Remarks**: Bouchet (1975b) placed this species in the genus *Cylichnium* Dall, 1908.

arachis. *Bulla arachis* Quoy *et* Gaimard, 1833: 361, pl. 26, figs 28-30. Type locality: "Port du Roi-Georges" (= King Georges Sound), Western Australia. SYNTYPE: 1 shell, leg. Quoy and Gaimard (Fig. 7F). **Remarks**: Pruvot-Fol (1934b) placed this species in the genus *Haminea* Leach, 1820.

brevis. *Bulla brevis* Quoy *et* Gaimard, 1833: 358, 359, pl. 26, figs 36, 37. Type locality: "Port du Roi-Georges" (= King Georges Sound), Western Australia. SYNTYPES: 10 shells, leg. Quoy and Gaimard (Fig. 7G). **Remarks**: Pruvot-Fol (1934b) placed this species in the genus *Haminea* Leach, 1820.

cymbalum. *Bulla cymbalum* Quoy *et* Gaimard, 1833: 362, pl. 26, figs 26, 27. Type locality: "Baie d'Humata" (= Umatac), Guam (Pacific

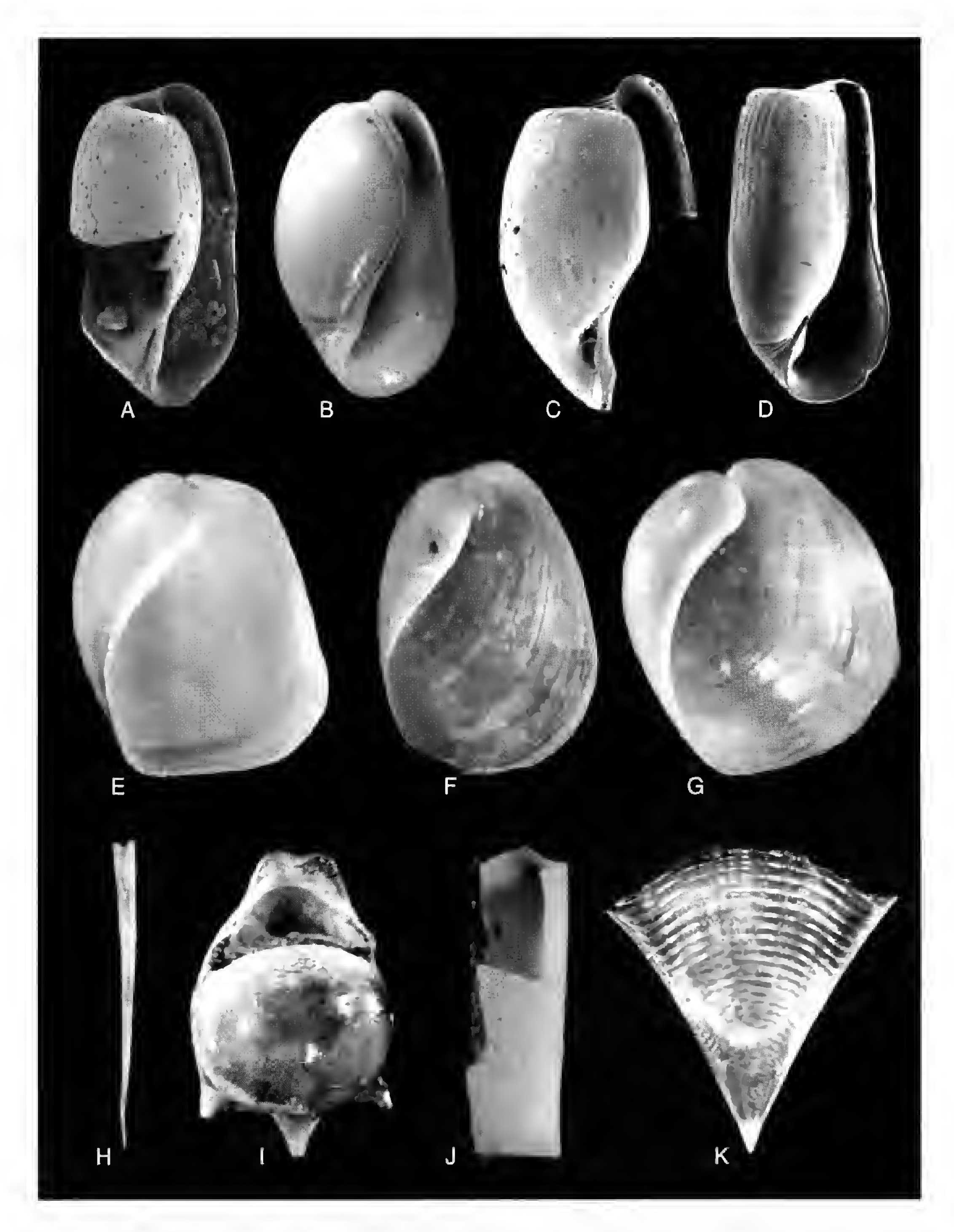


Fig. 6. — **A**, holotype of *Bulla girardi*, 2.4 mm; **B**, syntype of *Bulla simplex*, 10.7 mm; **C**, syntype of *Cylichnina tenerifensis*, 1.3 mm; **D**, syntype of *Cylichna truncatella*, 2.5 mm; **E**, holotype of *Philine azorica*, 7.5 mm; **F**, syntype of *Philine milneedwardsi*, 23.1 mm; **G**, holotype of *Philine monilifera*, 8.8 mm; **H**, lectotype of *Creseis acicula*, 12.6 mm; **I**, lectotype of *Hyalaea affinis*, 11.6 mm; **J**, syntype of *Cuvieria astesana*, 6.2 mm; **K**, holotype of *Cleodora chaptalii* Souleyet and *Clio chaptalii* J. E. Gray, 12.8 mm.

Ocean). SYNTYPE: 1 shell (broken), leg. Quoy and Gaimard (Fig. 7H). **Remarks**: This is the type species of the genus *Lamprohaminoea* Kuroda *et* Habe *in* Habe 1952, by original designation.

fischeri. *Aceras fischeri* Locard, 1897: 63-65, pl. 2, figs 10-14. Type locality: *Travailleur* (1880) Expedition, stn 10, 43°39'N - 03°28'W, Bay of Biscaye, 1960 m. SYNTYPES: 2 shells (1 broken) (Fig. 7I). **Remarks**: In acting as first revisor in the meaning of the Article 24 (ICZN 1985), Bouchet (1975b) determined that *Aceras africana* P. Fischer *in* Locard 1897 (placed in the genus *Cylichnium* Dall, 1908) has precedence over its subjective synonym *Aceras fischeri* Locard, 1897.

gallica. *Bulla gallica* Locard, 1905: 22, 23. Type locality: Atlantic and Mediterranean coast of France. SYNTYPES: 4 shells (Fig. 7J).

mongii. *Bulla mongii* Audouin, 1826: 39. Type locality: Egypt. HOLOTYPE (by monotypy, figured by Savigny 1817, pl. 5, fig. 7 and Bouchet & Danrigal 1982, fig. 58): shell (Fig. 4A).

orbignyana. *Bulla orbignyana* de Ferussac, 1822: 573. Type locality: La Rochelle, France. SYNTYPES: 4 shells (Fig. 4B).

ovoidea. *Bulla ovoidea* Quoy *et* Gaimard, 1833: 348, 349, pl. 26, figs 17-19. Type locality: "Plage d'Humata" (= Umatac), Guam (Pacific Ocean). SYNTYPE: 1 shell, leg. Quoy and Gaimard (Fig. 4C). **Remarks**: Pruvot-Fol (1934b) placed this species in the genus *Haminea* Leach, 1820.

perrieri. *Haminea perrieri* Morlet, 1889: 178, 179, pl. 6, fig. 7. Type locality: "Golfe de Siam" (= Gulf of Thailand). SYNTYPE: 1 shell, leg. Pavie (Fig. 4D).

waldae. *Cylichnium waldae* Bouchet, 1975b: 344-347, figs 11, 12, pl. 4, figs B, G. Type locality: *Walda* Expedition, stn CY15, 22°53'S - 11°56'E, Southeastern Atlantic, 1756 m. HOLOTYPE (by original designation, figured by Bouchet 1975b, pl. 4, fig. B): shell (Fig. 4E).

Family SMARAGDINELLIDAE Thiele, 1925

glauca. *Bulla glauca* Quoy *et* Gaimard, 1833: 352, 353, pl. 26, figs 10-12. Type locality: "Havre Carteret", New Ireland, Bismarck Archipelago. HOLOTYPE (by monotypy, figured by Quoy & Gaimard 1833, pl. 26, figs 10-12): specimen, leg. Quoy and Gaimard. **Remarks**: In acting as first revisor in the meaning of the Article 24 (ICZN 1985), Pruvot-Fol (1934b) determined that *Bulla viridis* Rang *in* Quoy & Gaimard 1833 (placed in the genus *Smaragdinella* A. Adams, 1848) has precedence over its sujective synonym *Bulla glauca* Quoy *et* Gaimard, 1833.

lutea. *Bulla lutea* Quoy *et* Gaimard, 1833: 369, 370, pl. 26, figs 40-44. Type locality: "Port Dorey" (= Manokwari), Irian Jaya, Indonesia. SYNTYPES: 4 specimens, leg. Quoy and Gaimard.

viridis. *Bulla viridis* Rang *in* Quoy & Gaimard 1833: 350-352, pl. 26, figs 13-16. Type locality: "Rade d'Humata" (= Umatac), Guam (Pacific Ocean). SYNTYPES: 22 specimens (6 of them dissected) and 3 shells, leg. Quoy and Gaimard. **Remarks**: This is the type species of the genus *Smaragdinella* A. Adams, 1848, by monotypy. According to Rudman (1972b), this is a junior synonym of *Smaragdinella calyculata* (Broderip *et* Sowerby, 1829).

Family BULLIDAE J. E. Gray, 1827

australis. *Bulla australis* de Ferussac, 1822: 573. Type locality: Port Jackson, Sydney, Australia. SYNTYPE: 1 shell (Fig. 3H).

australis. *Bulla australis* Quoy & Gaimard 1833: 357, 358, pl. 26, figs 38, 39. Type locality: "port du Roi-Georges" (= King Georges Sound), Western Australia. SYNTYPES (one figured by Quoy & Gaimard 1833, pl. 26, figs 38-39): 11 shells, leg. Quoy and Gaimard (Fig. 3I). **Remarks**: This name is preoccupied by *Bulla australis* de Ferussac, 1822.

delorti. *Bulla delorti* Mabille, 1896: 116. Type locality: Japan. SYNTYPES: 4 shells (Fig. 7A).

mabillei. *Bulla mabillei* Locard, 1897: 50, 51, pl. 2, figs 1, 2. Type locality: *Talisman* (1883) Expedition, stn 107 (no coordinates are specified), "Rade de Porte Grande" (= Porto Grande), São Vicente, Cape Verde Islands, 75-90 m. SYNTYPES (1 figured by Locard

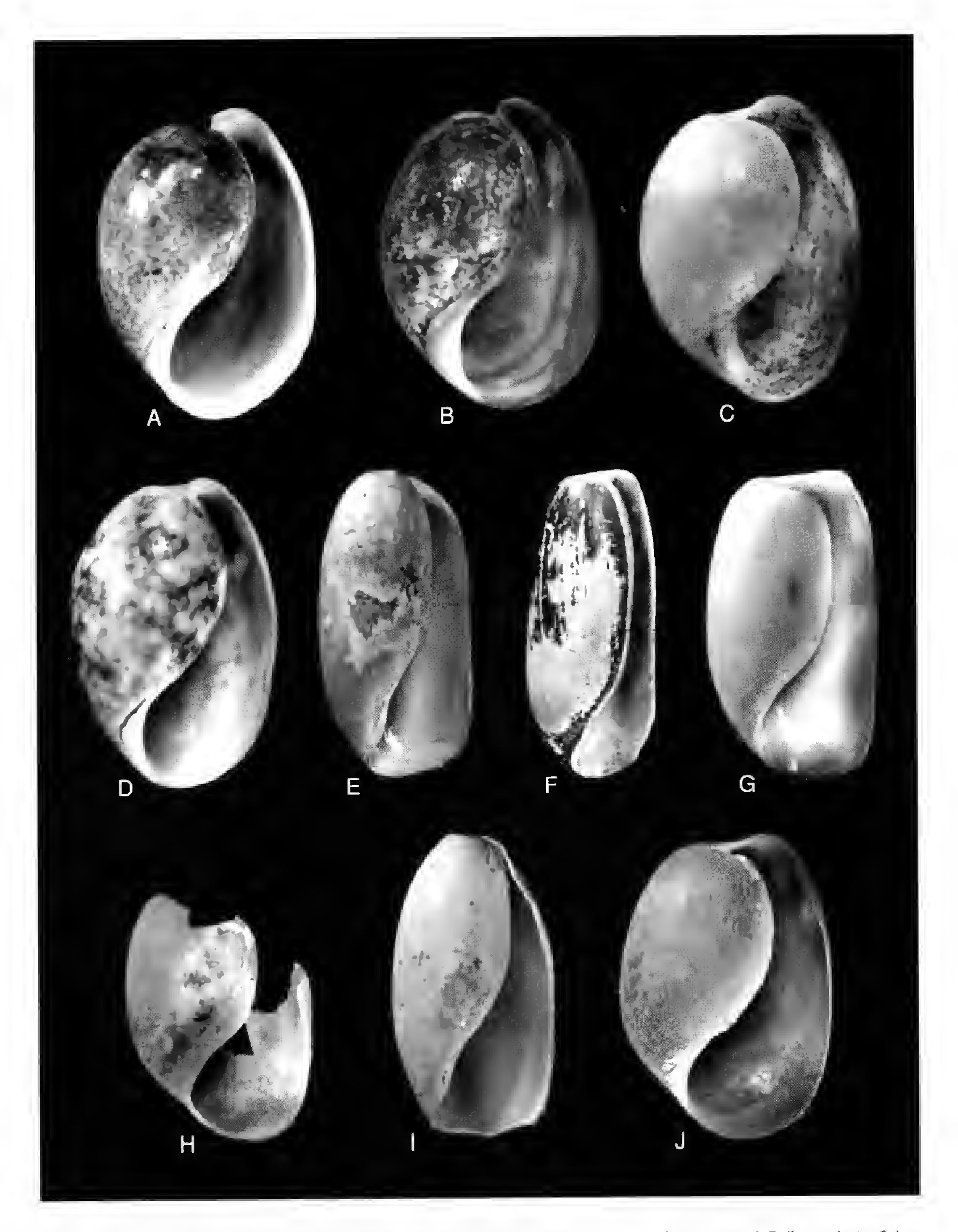


FIG. 7. — **A**, syntype of *Bulla delorti*, 35.2 mm; **B**, syntype of *Bulla mabillei*, 60.1 mm; **C**, syntype of *Bulla modesta*, 8.1 mm; **D**, syntype of *Bulla secunda*, 33.2 mm; **E**, syntype of *Aceras africana*, 15.8 mm; **F**, syntype of *Bulla arachis*, 17.7 mm; **G**, syntype of *Bulla brevis*, 12.6 mm; **H**, syntype of *Bulla cymbalum*, 26.6 mm; **I**, syntype of *Aceras fischeri*, 7.0 mm. **J**, syntype of *Bulla gallica*, 19.6 mm.

1897, pl. 26, figs 38, 39): 2 shells (Fig. 7B).

modesta. *Bulla modesta* Risso, 1826: 49, pl. 1, fig. 7. Type locality: Nice, France. SYNTYPES: 3 shells (1 broken) (Fig. 7C).

secunda. *Bulla secunda* Mabille, 1896: 112. Type locality: Japan. SYNTYPES: 6 shells (Fig. 7D).

Family RUNCINIDAE H. *et* A. Adams, 1854

coronata. *Pelta coronata* de Quatrefages, 1844: 151, 152, pl. 3, fig. 6, pl. 5, fig. 7, pl. 6, figs 3, 6, 9, 15. Type locality: Île de Bréhat, Bretagne, France. SYNTYPES: 4 specimens, leg. Quatrefages. **Remarks**: This is the type species of the genus *Pelta* Quatrefages, 1844, by original designation. The genus *Pelta* has been suppressed under plenary powers by Opinion 811 (ICZN 1967).

lenticula. *Runcina lenticula* Gofas, Ortea *et* Rodríguez, 1991: 541-545, figs 1-6. Type locality: Chapeu Armado, Namibe, Angola. HOLOTYPE (by original designation): specimen + 10 paratypes.

macrodenticulata. *Runcina macrodenticulata* García, García-Gómez *et* López, 1990: 4-6, fig. 1. Type locality: near Playa Benítez, Ceuta, Moroccan side of Strait of Gibraltar. HOLOTYPE (by original designation): specimen.

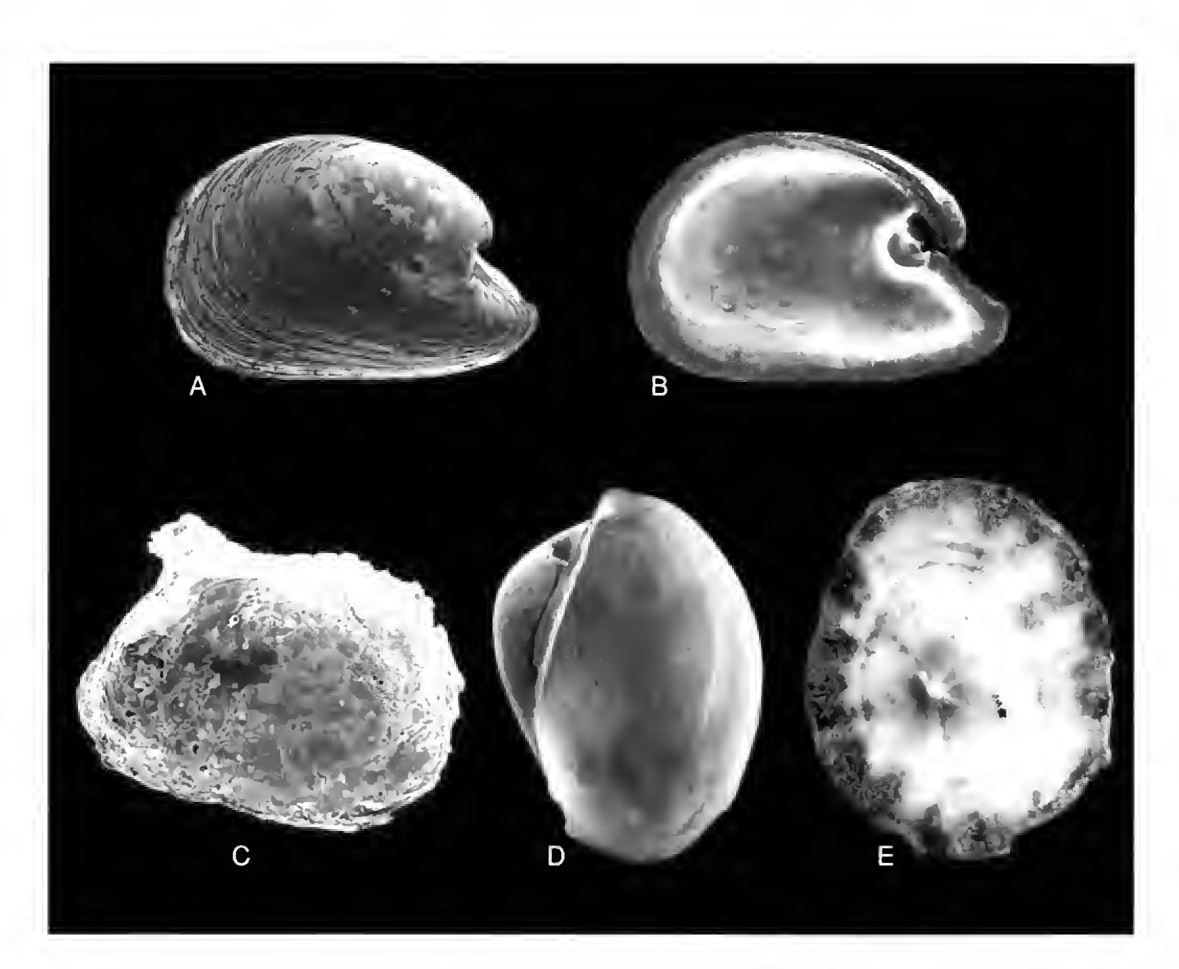


FIG. 8. — **A**, **B**, syntype of *Prasina borbonica*, 4.3 mm; **C**, syntype of *Berthelinia elegans*, 0.6 mm; **D**, holotype of *Lobiger souverbii*, 6.2 mm; **E**, syntype of *Umbrella cumingi*, 39.2 mm.

SACOGLOSSA

Family Oxynoeidae Stoliczka, 1868

sieboldii. *Lophocercus sieboldii* Krohn, 1847: 55-59, pl. 2, figs 5-9, 11. Type locality: Messina, Italy. SYNTYPES: 2 specimens (1 of them lacking shell). **Remarks**: This is the type species of the genus *Lophocercus* Krohn, 1847, by monotypy. After Mörch (1863b), *Lophocercus* is currently considered a synonym of *Oxynoe* Rafinesque, 1819.

souverbii. *Lobiger souverbii* P. Fischer, 1857: 273, 274, pl. 11, figs 7-10. Type locality: Guadeloupe (Caribbean Sea). HOLOTYPE (by monotypy, figured by P. Fischer 1857, pl. 11, figs 7, 8): shell (Fig. 8D).

Family Juliidae E. A. Smith, 1885

borbonica. *Prasina borbonica* Deshayes, 1863: 29, pl. 4, figs 4-8. Type locality: La Réunion (Indian Ocean). SYNTYPES: 2 shells (2 valves), 1 shell (1 valve), leg. Petit de la Saussaye (Fig. 8A, B). **Remarks**: This is the type species of the genus *Prasina* Deshayes, 1863, by monotypy, Kay (1968) placed *P. borbonica* in the genus *Julia* Gould, 1862, and suggested that it is probably a synonym of *J. exquisita* Gould, 1862.

elegans. *Berthelinia elegans* Crosse, 1875: 79, 80, pl. 2, fig. 3. Type locality: lower calcareous, Lutetian Stage (middle Eocene), Courtagnon, France. SYNTYPES (2 figured by Crosse, 1875, pl. 2, fig. 3): 7 shells (1 valve, considerably damaged), leg. Berthelin (Fig. 8C). **Remarks**: This is the type species of the genus *Berthelinia* Crosse, 1875, by monotypy.

Family Placobranchidae J. E. Gray, 1840

schrammi. *Tridachia schrammi* Mörch, 1863a: 41. Type locality: Guadeloupe (Caribbean Sea). SYNTYPES: 4 specimens. **Remarks**: Deshayes (1857) established the new genus *Tridachia* Deshayes, 1857, but did not name a species. Mörch (1863a) introduced for the first time the binominal name *Tridachia schrammi* in reference to Deshayes' description. *T. schrammi*, currently considered a synonym of *Elysia crispata* (Mörch, 1863), is the type species of the genus *Tridachia* Deshayes, 1857, by subsequent monotypy. Following Gosliner (1995), *Tridachia* is a junior synonym of *Elysia* Risso, 1818.

Family Hermaeidae H. *et* A. Adams, 1854

llerai. *Stiliger llerai* Ortea, 1982a: 188-191, figs 8, 9, pl. 1, fig. B. Type locality: El Prix, Tenerife, Canary Islands. HOLOTYPE (by original designation): specimen + spawn + photo.

lozanoi. *Ercolania lozanoi* Ortea, 1982a: 194-196, fig. 13. Type locality: Palm-Mar, Tenerife, Canary Islands. HOLOTYPE (by original designation, figured by Ortea 1982a, fig. 13): specimen.

verticilata. *Placida verticilata* Ortea, 1982a: 191-194, figs 10, 11, 12b. Type locality: Punta Hidalgo, Tenerife, Canary Islands. HOLOTYPE (by original designation): specimen.

APLYSIOMORPHA [= ANASPIDEA]

Family Akeridae Mazzarelli, 1891

bicincta. *Bulla bicincta* Quoy *et* Gaimard, 1833: 355, 356, pl. 26, figs 31, 32. Type locality: "Port du Roi-Georges" (= King Georges Sound), Western Australia. SYNTYPES: 2 shells glued to cardboard, severely broken, leg. Quoy and Gaimard.

elegans. *Acera elegans* Locard, 1886: 535. Type locality: Quiberon, France. SYNTYPES: 4 shells (3 broken) (Fig. 9I). **Remarks**: According to Lemche (1948), this is a junior subjective synonym of *Akera bullata* (Müller, 1776).

spirata. *Acera spirata* Staadt *in* Cossmann & Pissarro 1913, pl. 55, fig. 244-2. Type locality: Chenay, France (late Paleocene). HOLOTYPE (by monotypy, figured by Cossmann & Pissarro 1913, pl. 55, fig. 244-2): shell (Fig. 9J).

Family Aplysiidae Lamarck, 1809

alba. *Aplysiella gravieri* var. *alba* Vayssière,

1906b: 67, 68, pl. 4, figs 66-68. Type locality: Obock, Djibouti. HOLOTYPE (by monotypy, figured by Vayssière 1906b, pl. 4, figs 66-68): specimen (dissected) + some parts prepared for SEM. **Remarks**: According to Martínez (1996), this subspecific-rank taxon is a junior synonym of *Petalifera petalifera* (Rang, 1828).

ascifera. *Aplysia ascifera* Rang, 1828b: 51, 52, pl. 4, figs 7-9. Type locality: Saint Jean, Cayenne, French Guiana. SYNTYPES: 2 specimens, leg. Richard. **Remarks**: According to Engel & Hummelinck (1936), this is a junior synonym of *Dolabrifera dolabrifera* (Rang, 1828).

brasiliana. *Aplysia brasiliana* Rang, 1828b: 55, 56, pl. 8, figs 1-3. Type locality: Brazil. SYNTYPES: 3 specimens (2 of them dissected), leg. Quoy and Gaimard.

cirrhifera. *Aplysia cirrhifera* Quoy *et* Gaimard, 1832: 311, 312, pl. 24, fig. 8. Type locality: "Îles aux Cerfs", "Île de France" (= Mauritius), Indian Ocean. SYNTYPES: 2 specimens, leg. Quoy and Gaimard. **Remarks**: This is the type species of the subgenus *Barnardaclesia* Eales *et* Engel, 1935, by original designation.

dactylomela. *Aplysia dactylomela* Rang, 1828b: 56, pl. 9. Type locality: "Saint-Yago de la Praya" (= São Tiago), São Tiago Island, Praia, Cape Verde Islands. SYNTYPE: 1 specimen, leg. Rang. **Remarks**: This is the type species of the subgenus *Varria* Eales, 1960, by original designation.

ecaudata. *Aplysia ecaudata* Rang, 1828b: 47, pl. 2. Type locality: "Waigiou" (= Waigeo) and "Rawack" (= Gam), Irian Jaya, Indonesia. SYNTYPES: 3 specimens (1 of them dissected), leg. Quoy and Gaimard. **Remarks**: This is probably a junior synonym of *Dolabella auricularia* (Lightfoot, 1786).

gravieri. *Aplysiella gravieri* Vayssière, 1906b: 58-66, pl. 4, figs 56-65. Type locality: Gulf of Aden, Djibouti. HOLOTYPE (by monotypy, figured by Vayssière 1906b, pl. 4, figs 56-65 and Martínez 1996, fig. 10): specimen (dissected) + some parts prepared for SEM. **Remarks**: According to Martínez (1996), this is a junior synonym of *Petalifera petalifera* (Rang, 1828).

inca. *Aplysia inca* d'Orbigny, 1835: 207-209 (1837), pl. 19, figs 1-3 (1835). Type locality: between Callao and Islá de San Lorenzo, and Puerto de Lima, Perú. SYNTYPE: 1 specimen (dissected), leg. d'Orbigny.

juliana. *Aplysia juliana* Quoy *et* Gaimard, 1832: 309, 310, pl. 24, figs 5, 6. Type locality: "Île de France" (= Mauritius), Indian Ocean. SYNTYPES: 1 specimen (dissected) and 1 fragment of shell, leg. Quoy and Gaimard. **Remarks**: *Aplysia juliana* has been placed in the Official List of Specific Names in Zoology, Opinion 1844 (ICZN 1996). This is the type species of the subgenus *Tulia* Pruvot-Fol, 1934, by monotypy.

keraudrenii. *Aplysia keraudrenii* Rang, 1828b: 59, 60, pl. 13. Type locality: unknown. HOLOTYPE (by monotypy, figured by Rang, 1828b, pl. 13): specimen (dissected), leg. Lesson.

lessonii. *Aplysia lessonii* Rang, 1828b: 60, pl. 14. Type locality: Paita, Perú. SYNTYPE: 1 specimen (dissected and considerably damaged), leg. Lesson and Garnot. **Remarks**: According to Eales (1960), this could be a junior synonym of *Aplysia keraudrenii* Rang, 1828.

longicauda. *Aplysia longicauda* Quoy *et* Gaimard, 1824: 421, 422, pl. 66, fig. 8. Type locality: not specified; cited from "Île de France" (= Mauritius), Indian Ocean; "Îles Sandwich" (= Hawaii), "Baie des Chiens-Marins" (= Shark Bay), Australia; Rio de Janeiro, Brazil. SYNTYPE: 1 specimen.

maillardi. *Dolabrifera maillardi* Deshayes, 1863: 53, 54, pl. 7, figs 20-22. Type locality: La Réunion (Indian Ocean). SYNTYPES: 3 shells. **Remarks**: According to Engel & Hummelinck (1936), this is a junior synonym of *Dolabrifera dolabrifera* (Cuvier, 1817).

nudata. *Aplysia nudata* Rang, 1828b: 72, pl. 22, figs 3-5. Type locality: on floating algae near Hawaii. SYNTYPE: 1 specimen (dissected), leg. Quoy and Gaimard.

oahouensis. *Aplysia oahouensis* Souleyet, 1852: 461, 462, pl. 25, 10-13. Type locality: Oahu, "Îles Sandwich" (= Hawaii). SYNTYPE: 1 specimen, leg. Eydoux and Souleyet. **Remarks**: According to Engel & Hummelinck (1936), this could be a junior synonym of *Dolabrifera dolabrifera* (Rang, 1828).

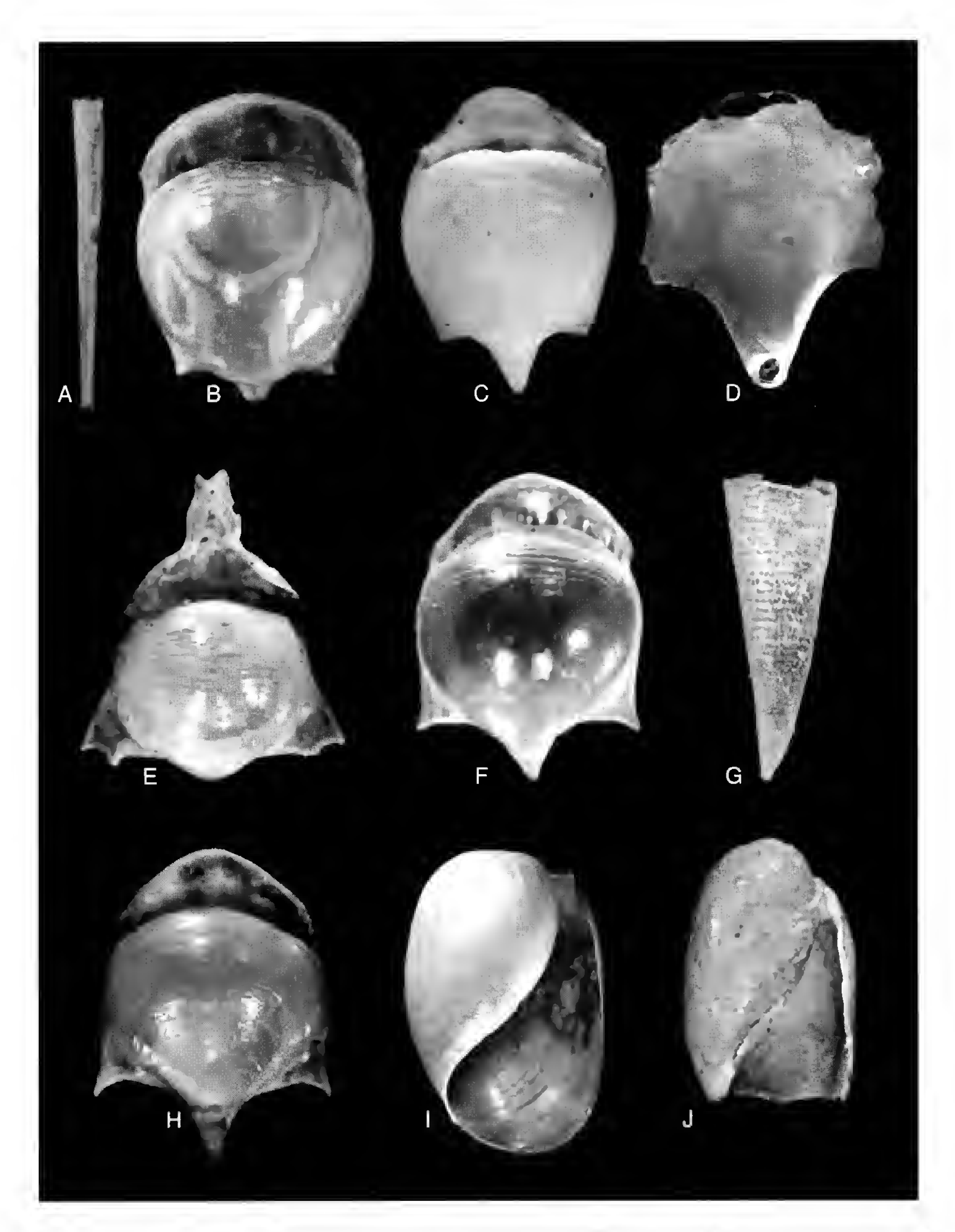


FIG. 9. — **A**, lectotype of *Creseis clava*, 10.0 mm; **B**, lectotype of *Hyalaea gibbosa*, 7.2 mm; **C**, syntype of *Hyalaea globulosa* and lectotype of *Cavolina globulosa*, 6.2 mm; **D**, syntype of *Hyalaea levigata*, 2.0 mm; **E**, lectotype of *Hyalaea limbata*, 7.9 mm; **F**, syntype of *Hyalea rangii*, 8.3 mm; **G**, syntype of *Creseis striata*, 5.7 mm; **H**, lectotype of *Hyalea uncinata*, 7.6 mm; **I**, syntype of *Acera elegans*, 21.6 mm; **J**, holotype of *Acera spirata*, 17.2 mm.

petalifera. *Aplysia petalifera* Rang, 1828b: 52, pl. 5, figs 1-3. Type locality: Nice, France. SYNTYPES: 2 specimens (dissected), leg. Risso. **Remarks**: This is the type species of the genus *Petalifera* J. E. Gray, 1847, by absolute tautonymy.

pleei. *Aplysia pleei* Rang, 1828b: 70, pl. 21. Type locality: Antilles. SYNTYPE: 1 specimen (dissected), leg. Plée. **Remarks**: According to Eales & Engel (1935), this name must be used for a subspecies of *Bursatella leachii* de Blainville, 1817 occuring throughout the Caribbean Sea.

protea. *Aplysia protea* Rang, 1828b: 56, 57, pl. 10, figs 1-3. Type locality: Antilles. SYNTYPES: 3 specimens (1 of them dissected), leg. Richard; 2 specimens (dissected), leg. Plée. **Remarks**: According to Eales (1960), this is a junior synonym of *Aplysia dactylomela* Rang, 1828.

rufa. *Aplysia rufa* Quoy *et* Gaimard, 1832: 314, pl. 24, fig. 7. Type locality: "rade d'Umata" (= Bay of Umatac), Guam (Pacific Ocean). SYNTYPE: 1 specimen (dissected), leg. Quoy and Gaimard.

striata. *Aplysia striata* Quoy *et* Gaimard, 1832: 315, 316, pl. 24, figs 9-11. Type locality: "Port Dorey" (= Manokwari), Irian Jaya, Indonesia. SYNTYPE: 1 specimen, leg. Quoy and Gaimard. **Remarks**: In the original description of this species, Quoy & Gaimard (1832) noted that it is probably the same as *Stylocheilus longicauda* (Quoy *et* Gaimard, 1824).

teremidi. *Aplysia teremidi* Rang, 1828b: 48, pl. 3, figs 1-3. Type locality: not specified; cited from Tahiti and Bora Bora, Society Islands (Pacific Ocean); Oualan, Caroline Islands (Pacific Ocean). SYNTYPE: 1 specimen, leg. Lesson and Garnot. **Remarks**: This is probably a junior synonym of *Dolabella auricularia* (Lightfoot, 1786).

tongana. *Aplysia tongana* Quoy *et* Gaimard, 1832: 305, 306, pl. 23, figs 6, 7. Type locality: "Île de Pangaï-Modou", Tongatapu (Pacific Ocean). SYNTYPE: 1 specimen (dissected), leg. Quoy and Gaimard. **Remarks**: This is probably a junior synonym of *Dolabella auricularia* (Lightfoot, 1786).

unguifera. *Aplysia unguifera* Rang, 1828b: 52, pl. 5, figs 4-7. Type locality: Mediterranean Sea. SYNTYPES: 2 specimens (1 of them dissected), leg. Risso. **Remarks**: According to Engel & Hummelinck (1936), this is a junior synonym of *Petalifera petalifera* (Rang, 1828).

NOTASPIDEA

Family UMBRACULIDAE Dall, 1889

cumingi. *Umbrella cumingi* Deshayes, 1863: 52, 53, pl. 8, figs 4, 5. Type locality: La Réunion (Indian Ocean). SYNTYPES: 3 shells (Fig. 8E).

Family PLEUROBRANCHIDAE J. E. Gray, 1827

amboinei. *Oscaniopsis amboinei* Vayssière, 1900: 9, 10. Type locality: Ambon, Moluccas, Indonesia. SYNTYPES: 2 specimens, one of them dissected. **Remarks**: According to Ev. Marcus & Gosliner (1984), this is a junior synonym of *Euselenops luniceps* (Cuvier, 1817).

brocki. *Berthella brocki* Vayssière, 1897a: 120-122, pl. 5, figs 8-10. Type locality: not specified; cited from Ambon, Moluccas, Indonesia; Edam, near Jakarta, Indonesia; Jervis Bay, Australia. SYNTYPES: 8 specimens (2 of them dissected).

capensis. *Pleurobranchaea capensis* Vayssière, 1900: 10, 11. Type locality: Cape of Good Hope, Southern Africa. SYNTYPE: 1 specimen (considerably damaged), leg. Raynaud. **Remarks**: According to Ev. Marcus & Gosliner (1984), this is a junior synonym of *Pleurobranchea tarda* Verrill, 1880.

citrinus. *Pleurobranchus citrinus* Rüppell *et* Leuckart, 1828: 20, pl. 5, figs 1A-C. Type locality: Suez, Egypt. SYNTYPES: 2 specimens (1 of them dissected), leg. Rüppell. **Remarks**: This species is currently placed in the genus *Berthellina* Gardiner, 1936.

crossei. *Pleurobranchus crossei* Vayssière, 1897b: 353, 354, fig. 1. Type locality: Caribbean Sea. HOLOTYPE (by monotypy, figured by Vayssière 1897b, fig. 1): specimen (dissected), leg. Plée.

digueti. *Pleurobranchus digueti* de Rochebrune, 1895: 240. Type locality: Mogote, Bahía de La

Paz, Mexico. SYNTYPES: 4 specimens, leg. Diguet.

giardi. *Pleurobranchus giardi* Vayssière, 1897b: 354-356, fig. 2. Type locality: Camiguin, Luzon, Philippines. SYNTYPE: 1 specimen (dissected), leg. Semper.

maculatum. *Pleurobranchidium maculatum* Quoy *et* Gaimard, 1832: 301, 302, pl. 22, figs 11-14. Type locality; Southern Australia. SYNTYPES: 7 specimens (4 of them dissected), leg. Quoy and Gaimard. **Remarks**: Ev. Marcus & Gosliner (1984) placed this species in the genus *Pleurobranchaea* Meckel *in* Leue 1813.

mamillatus. *Pleurobranchus mamillatus* Quoy *et* Gaimard, 1832: 294-296, pl. 22, figs 1-6. Type locality: Port Louis, "Île de France" (= Mauritius), Indian Ocean. SYNTYPES: 2 specimens (dissected).

peronii. *Pleurobranchus peronii* Cuvier, 1804b: 275, 276, pl. 18, figs 1-6. Type locality: "Mer des Indes" (= Indian Ocean). SYNTYPE: 1 specimen, leg. Peron. **Remarks**: This is the type species of the genus *Pleurobranchus* Cuvier, 1804, by monotypy.

perrieri. *Pleurobranchus perrieri* Vayssière, 1897a: 126-128, pl. 4, figs 2-4. Type locality: not specified; cited from Philippines; Ambon, Moluccas, Indonesia; Tahiti. SYNTYPES: 16 specimens (12 of them dissected).

vayssierei. *Pleurobranchaea vayssierei* Ev. Marcus *et* Gosliner, 1984: 38, 39, fig. 19. Type locality: Alger, Algeria. HOLOTYPE (by original designation, figured by Ev. Marcus & Gosliner 1984, fig. 19): specimen (dissected), leg. Vayssière + radula, jaws and reproductive system slides.

THECOSOMATA

Family CAVOLINIIDAE J. E. Gray, 1850

acicula. *Creseis acicula* Rang, 1828a: 317, pl. 17, fig. 6. Type locality: "Mer des Indes" (= Indian Ocean). LECTOTYPE (selected by van der Spoel 1976: 189): shell (Fig. 6H) + 18 paralectotypes (broken).

affinis. *Hyalaea affinis* d'Orbigny, 1834: 91-93, pl. 5, figs 6-10. Type locality: approximately between 30° to 34°S and 78° to 90°W (Pacific Ocean). LECTOTYPE (selected by van der Spoel, 1976: 194): shell, leg. d'Orbigny (Fig. 6I) + 1 paralectotype. **Remarks**: According to van der Spoel (1967; 1976), this nominal species is merely the form *affinis* of *Cavolinia tridentata* (Forsskål *in* Niebuhr 1775).

angulata. *Hyalaea angulata* Souleyet, 1852: 152, 153, pl. 5, figs 1-6. Type locality: not specified; cited from Atlantic, Indian Ocean and Sea of China. SYNTYPE: 1 specimen, from Indian Ocean, leg. Eydoux and Souleyet. **Remarks**: See comments on *Cavolina angulosa* J. E. Gray, 1850.

angulosa. *Cavolina angulosa* J. E. Gray, 1850: 8. Type locality: Indian Ocean. LECTOTYPE (selected by van der Spoel 1976: 193): specimen, leg. Eydoux and Souleyet. **Remarks**: Eydoux & Souleyet (1846-1849) figured this species under the vernacular French name "Hyale angulée". J. E. Gray (1850) is the first author who introduced the name *Cavolina angulosa* under binominal nomenclature, without description, but referring to the figures in the Atlas of Eydoux & Souleyet. However, J. E. Gray incorrectly made reference to pl. 4, figs 1-6, whereas Eydoux & Souleyet (1846-1849) figured this species in pl. 5, figs 1-6. This is certain to be a typographical error because J. E. Gray explicitly mentioned the name "Hyale angulée". Later, Souleyet (1852) established *Hyalaea angulata* as a new species, giving a description and a reference to the same figures. Therefore, this is a case of independent latinization of the same name. Van der Spoel *et al.* (1993) placed this species in the genus *Diacavolinaia* van der Spoel, 1987.

astesana. *Cuvieria astesana* Rang, 1829b: 498, 499, pl. 19, fig. B. Type locality: "l'Astésan" (= Asti), Italy (Pliocene). SYNTYPE: 1 shell (broken) (Fig. 6J).

chaptalii. *Cleodora chaptalii* Souleyet, 1852: 183, 184, pl. 7, figs 1-5. Type locality: Cape of Good Hope (Southern Africa). HOLOTYPE (by monotypy, figured by Eydoux & Souleyet 1846-1849, pl. 7, figs 1-5): shell, leg. Eydoux

and Souleyet (Fig. 6K). **Remarks**: See remarks under *Clio chaptalii* J. E. Gray, 1850.

chaptalii. *Clio chaptalii* J. E. Gray, 1850: 14. Type locality: Cape of Good Hope (Southern Africa). HOLOTYPE (by monotypy, figured by Eydoux & Souleyet 1846-1849, pl. 7, figs 1-5): shell, leg. Eydoux and Souleyet (Fig. 6K). **Remarks**: Eydoux & Souleyet (1846-1849, pl. 7, figs 1-5) figured this species under the vernacular French name "Cléodore de Chaptal". J. E. Gray (1850) is the first author who introduced the name *Clio chaptalii* under binominal nomenclature, without a description, but referring to the figures in the Atlas of Eydoux & Souleyet. Later, Souleyet (1852) described *Cleodora chaptalii* as a new species, giving a description and a reference to the same figures. Therefore, this is a case of independent latinization of the same name. Since both species are based on the same single specimen, *Cleodora chaptalii* Souleyet, 1852 is an objective junior synonym of *Clio chaptalii* J. E. Gray, 1850. In addition, they are secondary homonyms. According to van der Spoel (1967, 1976), this nominal species is just the form *major* of *Diacria trispinosa* (Lesueur, 1821).

clava. *Creseis clava* Rang, 1828a: 317, pl. 17, fig. 5. Type locality: Agulhas Bank, Southern Africa. LECTOTYPE (selected by van der Spoel, 1976: 189): shell (Fig. 9A) + 4 paralectotypes. **Remarks**: According to van der Spoel (1967: 59), this nominal species is merely a form *clava* of *Creseis acicula* Rang, 1828.

gibbosa. *Hyalaea gibbosa* Rang *in* d'Orbigny 1834: 95, 96, pl. 5, figs 16-20. Type locality: not specified; cited from approximately between 34°N to 40°S and 26° to 43°W (Atlantic Ocean). LECTOTYPE (selected by van der Spoel, 1976: 195): shell, leg. d'Orbigny (Fig. 9B) + 3 paralectotypes. **Remarks**: According to van der Spoel (1967; 1976), this species belongs to the genus *Cavolinia* Abildgaard, 1791.

globulosa. *Hyalaea globulosa* Rang *in* Souleyet 1852: 142, 143, pl. 4, figs 20-24. Type locality: not specified; cited from Pacific, Atlantic, Indian Ocean and Sea of China. SYNTYPES: 5 shells (Fig. 9C) from "Nouvelle Hollande" (= Australia), leg. Rang. **Remarks**: See remarks under *Cavolina globulosa* J. E. Gray, 1850.

globulosa. *Cavolina globulosa* J. E. Gray, 1850: 8. Type locality: not specified; cited from Pacific, Atlantic, Indian Ocean and Sea of China. LECTOTYPE (selected by van der Spoel, 1976: 196): shell (Fig. 9C) + 4 paralectotypes from "Nouvelle Hollande" (= Australia), leg. Rang. **Remarks**: Eydoux & Souleyet (1846-1849, pl. 4, figs 20-24) figured this species under the vernacular French name "Hyale globuleuse". J. E. Gray (1850) is the first author who introduced the name *Cavolina globulosa* under binominal nomenclature, without a description, but citing to the figures in the Atlas of Eydoux & Souleyet. Later, Rang *in* Souleyet (1852) described *Hyalaea globulosa* as a new species, giving a description and a reference to the same figures. Therefore, this is a case of independent latinization of the same name. Both nominal species *Cavolina globulosa* J. E. Gray, 1850 and *Hyalaea globulosa* Rang *in* Souleyet 1852 are secondary homonyms.

inflata. *Cleodora inflata* Souleyet, 1852: 188, pl. 7, figs 17-19. Type locality: Atlantic Ocean. SYNTYPE: 1 specimen, leg. Eydoux and Souleyet. **Remarks**: See remarks on *Balantium inflatum* J. E. Gray, 1850.

inflatum. *Balantium inflatum* J. E. Gray, 1850: 15. Type locality: Atlantic Ocean. SYNTYPE: 1 specimen, leg. Eydoux and Souleyet. **Remarks**: Eydoux & Souleyet (1846-1849, pl. 7, figs 17-19) figured this species under the vernacular French name "Cléodore renflée". J. E. Gray (1850) is the first author who introduced the name *Balantium inflatum* under binominal nomenclature, without a description, but citing to the figures in the Atlas of Eydoux & Souleyet. Later, Souleyet (1852) described *Cleodora inflata* as a new species, independenly giving a description and a reference to the same figures. Therefore, this is a case of independent latinization of the same name. Since both species are based on the same type material, *Cleodora inflata* Souleyet, 1852 is an objective junior synonym of *Balantium inflatum* J. E. Gray, 1850. In addition, they are secondary homonyms. According to van der Spoel (1967: 76), this could be a synonym of *Clio recurva* (Children, 1823).

levigata. *Hyalaea levigata* d'Orbigny, 1834: 110, 111, pl. 7, figs 15-19. Type locality: not specified; cited from approximately 20°S, 87°W (Pacific Ocean). SYNTYPE (figured by d'Orbigny 1835, pl. 7, figs 15-19): 1 shell juvenile, leg. d'Orbigny (Fig. 9D). **Remarks**: According to van der Spoel *et al.* (1993), this is probably a junior synonym of *Diacavolinia longirostris* (Lesueur, 1821).

limbata. *Hyalaea limbata* d'Orbigny, 1834: 101-103, pl. 6, figs 11-15. Type locality: not specified; cited from approximately between 30° to 33°S and 80° to 90°W (Pacific Ocean), and approximately between 12°N to 24°S and 25° to 28°W (Atlantic Ocean). LECTOTYPE (selected by van der Spoel, 1976: 193): shell, from Atlantic Ocean, leg. d'Orbigny (Fig. 9E) + 2 paralectotypes. **Remarks**: Van der Spoel *et al.* (1993) placed this species in the genus *Diacavolinia* van der Spoel, 1987.

longicaudatus. *Clio longicaudatus* Souleyet, 1852: 286-288, pl. 14, figs 17-21. Type locality: approximately 10°N - 21°W (Atlantic Ocean). SYNTYPE: 1 specimen, leg. Eydoux and Souleyet. **Remarks**: This is the type species of the genus *Clionina* Pruvot-Fol, 1924, by monotypy.

oblonga. *Clio oblonga* Rampal, 1997: 175-185, Pl. 1, figs A-I. Type locality: Tyrrhenian Sea, 39°36'N - 13°49'E, 2103 m (Quaternary). HOLOTYPE: 1 shell (figured by Rampal, 1997: pl, 1, figs A-D) + 3 paratypes.

orbignii. *Hyalea orbignii* Rang, 1827: 383. Type locality: Saint-Paul-les-Dax (lower Miocene: Burdigalian, France). HOLOTYPE: van der Spoel (1976: 192) records the holotype to be present in MNHN, but this specimen is currently untraceable.

rangii. *Hyalea rangii* Deshayes, 1831: 310. Type locality: coast of Africa. SYNTYPES: 5 shells (Fig. 9F). **Remarks**: According to van der Spoel (1967), this is a junior synonym of *Cavolinia tridentata* (Forsskål *in* Niebuhr 1775).

striata. *Creseis striata* Rang 1828a: 314, 315, pl. 17, fig. 3. Type locality: not specified; cited from Atlantic and Indian Oceans. SYNTYPES: 9 shells (broken) (Fig. 9G). **Remarks**: This is the type species of the genus *Hyalocylis* de Folin, 1875, by monotypy.

uncinata. *Hyalea uncinata* Rang, 1829a: 114. Type locality: unknown. LECTOTYPE (selected by van der Spoel, 1976: 195): shell (Fig. 9H) + 11 paralectotypes. **Remarks**: Van der Spoel (1987: 78) placed this species in the genus *Cavolinia* Abildgaard, 1791.

Family CYMBULIIDAE J. E. Gray, 1840

ovata. *Cymbulia ovata* Quoy *et* Gaimard, 1833: 373, 374, pl. 27, figs 25-30. Type locality: Amboine, Indonesia. LECTOTYPE (selected by van der Spoel, 1976: 198): specimen, leg. Quoy and Gaimard + 7 paralectotypes. **Remarks**: Van der Spoel (1976: 41) placed this species in the genus *Corolla* Dall, 1871.

NUDIBRANCHIA-DORIDINA

Family GONIODORIDIDAE H. *et* A. Adams, 1854

darwini. *Thecacera darwini* Pruvot-Fol, 1950: 49-51, figs 1-4. Type locality: "Baie Orange", Bahía de Nassau, Chile. SYNTYPES: 7 specimens (1 of them dissected).

pilosa. *Hopkinsia pilosa* Bouchet *et* Ortea, 1983: 227-231, figs 1-7. Type locality: Nguetu Reef, New Caledonia. HOLOTYPE (by original designation): specimen + 1 paratype.

polycerelloides. *Bermudella polycerelloides* Ortea *et* Bouchet, 1983: 50-54, figs 1, 2. Type locality: Los Cristianos, Tenerife, Canary Islands. HOLOTYPE (by original designation): specimen + 1 paratype.

savignyi. *Goniodoris savignyi* Pruvot-Fol, 1933: 117, 118, pl. 2, figs 23-26. Type locality: Gulf of Suez, Egypt. HOLOTYPE (by monotypy, figured by Pruvot-Fol, 1933, pl. 2, figs 23-26): specimen (dissected), leg. Dollfus. **Remarks**: This is the type species of the subgenus *Goniodoridella* Pruvot-Fol, 1933, by monotypy.

violacea. *Goniodoris violacea* Risbec, 1928: 177-179, fig. 53, pl. 7, fig. 5. Type locality: Pointe de l'Artillerie, Nouméa, New Caledonia. HOLOTYPE (by monotypy, figured by Risbec, 1928, fig. 53, pl. 7, fig. 5): specimen (dissected). **Remarks**: In the figure caption of pl. 7, fig. 5, this is cited as *Chromodoris violacea*.

Family ONCHIDORIDIDAE Gray, 1827

reticulata. *Onchidoris reticulata* Ortea, 1979b: 169-173, fig. 2. Type locality: Concha de Artedo, Asturias, Spain. HOLOTYPE (by original designation, figured by Ortea 1979b, fig. 2): specimen + photo.

tridactila. *Onchidoris tridactila* Ortea *et* Ballesteros, 1982: 241-246, figs 2, 3 (in part), 7 (in part), 8 B, C. Type locality: Verdicio, Asturias, Spain. HOLOTYPE (by original designation): specimen.

Family POLYCERIDAE Adler *et* Hancock, 1845

fulgurans. *Plocamopherus fulgurans* Risbec, 1928: 206-208, fig. 63, pl. 4, fig. 4. Type locality: Nouméa and Bourail, New Caledonia. SYNTYPE: 1 specimen.

gulo. *Plocamopherus gulo* Ev. Marcus, 1979: 134-136, figs 7-12. Type locality: *Calypso* Expedition, stn 145, 26°34'S - 47°22'W, between Parana and Santa Catarina, Brazil, 100 m. HOLOTYPE (by monotypy, figured by Ev. Marcus 1979, figs 7-12): specimen (considerably damaged) + radula and jaws slide.

picta. *Polycera picta* Risbec, 1928: 200-202, fig. 61, pl. 7, fig. 6, Type locality: Pointe de l'Artillerie (Nouméa) and Bourail, New Caledonia. SYNTYPES: 2 specimens.

Family GYMNODORIDIDAE Odhner, 1941

ceutae. *Tambja ceutae* García-Gómez *et* Ortea, 1988: 302-305, figs 1-7, pl. 1. Type locality: El Pineo, Ceuta, Spain. HOLOTYPE (by original designation, figured by García-Gómez & Ortea 1988, figs 1-7, pl. 1): specimen (dissected) + radula slide.

europaea. *Roboastra europaea* García-Gómez, 1985: 169-174, figs 1-5. Type locality: Tarifa, Spain. HOLOTYPE (by original designation): specimen.

perlucens. *Trevelyana perlucens* Risbec, 1928: 185-189, fig. 57, 57bis, pl. 1, fig. 12, pl. 5, fig. 1. Type locality: New Caledonia. SYNTYPES: 3 specimens.

suggens. *Trevelyana suggens* Risbec, 1928: 190-193, fig. 58, pl. B, fig. 1, pl. 5, figs 3, 6, pl. 7, fig. 10. Type locality: "Tembia" (= Timbia) and Nouméa, New Caledonia. SYNTYPES: 2 specimens.

Family VAYSSIEREIDAE Thiele, 1931

caledonica. *Vayssierea caledonica* Risbec, 1928: 290-292, fig. 98, pl. 12, fig. 8. Type locality: New Caledonia. SYNTYPES: 6 specimens. **Remarks**: This is the type species of the genus *Vayssierea* Risbec, 1928, by monotypy.

Family HEXABRANCHIDAE Bergh, 1891

lacera. *Doris lacera* Cuvier, 1804a: 452-465, 473, pl. 73, figs 1-3. Type locality: Timor, Indonesia. SYNTYPES: 2 specimens (dissected), leg. Péron and Lesueur. **Remarks**: Pruvot-Fol (1934a) placed this species in the genus *Hexabranchus* Ehrenberg, 1831.

sandwichiensis. *Doris sandwichiensis* Souleyet, 1852: 451, 452, pl. 25, figs 1-4. Type locality: "Îles Sandwich" (= Hawaii). SYNTYPE: 1 specimen (dissected), leg. Eydoux and Souleyet. **Remarks**: According to Thompson (1972), this is a junior synonym of *Hexabranchus sanguineus* (Rüppell *et* Leuckart, 1828).

Family DORIDIDAE Rafinesque, 1815

aspera. *Staurodoris aspera* Risbec, 1928: 101, 102, fig. 20, pl. 2, fig. 8. Type locality: Baie de Plum and Nouméa, New Caledonia. SYNTYPE: 1 specimen.

immonda. *Platydoris immonda* Risbec, 1928: 84, 85, fig. 12, pl. 1, fig. 4. Type locality: New Caledonia. SYNTYPE: 1 specimen. **Remarks**: According to Brodie & Willan (1993), this is a junior synonym of *Sirains nucleola* (Pease, 1860).

lophatus. *Thorybopus lophatus* Bouchet, 1977: 43-46, figs 11-13, pl. 1, fig. D. Type locality: *Biaçores* Expedition, stn 241, 37°37N - 25°32W, off Santa Maria, Azores, 395-465 m. HOLOTYPE (by original designation, figured by Bouchet, 1977, figs 11-13, pl. 1, fig. D): specimen (dissected). **Remarks**: This is the type species of the genus *Thorybopus* Bouchet, 1977, by original designation.

Family ARCHIDORIDIDAE Bergh, 1892

antarctica. *Archidoris tuberculata* var. *antarctica* Vayssière, 1917: 16, 17. Type locality: between "Île Jenny" and "Terre Adélaïde", Marguerite Bay (Antarctica). SYNTYPES: 3 specimens (dissected). **Remarks**: According to Wägele (1993), this subspecific-rank taxon is a junior synonym of *Austrodoris kerguelenensis* (Bergh, 1884).

carinata. *Doris carinata* Quoy *et* Gaimard, 1832: 254, pl. 16, figs 10-14. Type locality: "rivière Tamise" (= Thames), New Zealand. SYNTYPE: 1 specimen. **Remarks:** This is the type species of the genus *Atagema* J. E. Gray, 1850, by monotypy.

flava. *Guyonia flava* Risbec, 1928: 103, 104, fig. 21, pl. 3, fig. 6. Type locality: New Caledonia. SYNTYPE: 1 specimen.

granulatissima. *Archidoris granulatissima* Vayssière, 1917: 17-19, pl. 4, figs 43, 44. Type locality: "Dragage IX" (coordinates unknown), Adelaide Island, and "Baie de l'Amirauté", King Georges Island, Antarctica. SYNTYPES: 4 specimens (dissected). **Remarks**: According to Wägele (1993), this is a junior synonym of *Austrodoris kerguelenensis* (Bergh, 1884).

odonoghuei. *Archidoris odonoghuei* Pruvot-Fol, 1933: 118-120, pl. 2, figs 18-22. Type locality: Gulf of Suez, Egypt. SYNTYPES: 3 specimens (dried), leg. Dollfus.

paagoumenei. *Phlegmodoris paagoumenei* Risbec, 1928: 87-90, fig. 15, pl. B, fig. 3, pl. 3, fig. 1. Type locality: Paagoumène, New Caledonia. HOLOTYPE (by monotypy): radula.

schembrii. *Doris schembrii* Verany, 1846: 97, 101, 102. Type locality: Gulf of Genova (Mediterranean Sea). SYNTYPES: 2 specimens. **Remarks**: This is the only specimen of the Verany opisthobranch collection which could be located. It seems to have been borrowed by Vayssière and later was deposited in MNHN. The remainder of the Verany collection is probably lost.

vayssierea. *Archidoris vayssierea* O'Donoghue, 1929: 812-814, fig. 223. Type locality: Suez Canal, Egypt. SYNTYPE (figured by Vayssière, 1912, pl. 2, figs 27-29): 1 specimen (dissected), leg. Gravier. **Remarks**: O'Donoghue (1929) introduced the name *Archidoris vayssierea* based on one specimen reported by Vayssière (1912) from the Suez Canal (under the name *Archidoris staminea* Basedow *et* Hedley, 1905) and deposited in MNHN, and another specimen of his own collection from this area. Both specimens are syntypes of this species.

Family BAPTODORIDIDAE Odhner, 1926

boucheti. *Carminodoris boucheti* Ortea, 1979c: 579-582, figs 5-7. Type locality: Concha de Artedo, Asturias, Spain. HOLOTYPE (by original designation): specimen.

ceneris. *Paradoris ceneris* Ortea, 1995: 21-25, figs 1A, 1E, 13-15. Type locality: Puerto de Arrecife, Lanzarote, Canary Islands. HOLOTYPE (by original designation, figured by Ortea 1995, figs 1A, 1E, 13-15): specimen (dissected).

fongosa. *Baptodoris fongosa* Risbec, 1928: 111-115, fig. 25, pl. 2, fig. 9, pl. 3, fig. 9. Type locality: New Caledonia. SYNTYPES: 2 specimens + spawn.

inversa. *Paradoris inversa* Ortea, 1995: 14-17, figs 1C, 6-8. Type locality: El Médano, Tenerife, Canary Islands. HOLOTYPE (by original designation, figured by Ortea 1995, fig. 6A): specimen.

mollis. *Paradoris mollis* Ortea, 1995: 18-21, figs 1B, 9-12. Type locality: Adeje, Tenerife, Canary Islands. HOLOTYPE (by original designation, figured by Ortea 1995, figs 1B, 9-12): specimen (dissected).

perezi. *Baptodoris perezi* Llera *et* Ortea *in* Ortea *et al.* 1982: 24-29, figs 9-11, pl. 1, fig. C. Type locality: Playa de San Juan, Tenerife, Canary Islands. HOLOTYPE (by original designation): specimen.

Family DISCODORIDIDAE Bergh, 1891

ascitica. *Taringa ascitica* Ortea, Pérez-Sánchez *et* Llera, 1982: 34-38, figs 15-17, pl. 2, fig. H. Type locality: La Isleta, Lanzarote, Canary Islands. HOLOTYPE (by original designation, figured by Ortea *et al.* 1982, figs 15-17, pl. 2, fig. H): specimen (dissected).

bacalladoi. *Geitodoris bacalladoi* Ortea, 1990:

116-119, figs 12-14. Type locality: Agua Dulce, Tenerife, Canary Islands. HOLOTYPE (by original designation): specimen + 1 paratype.

bacalladoi. *Taringa bacalladoi* Ortea, Pérez-Sánchez *et* Llera, 1982: 42-45, figs 20-22, pl. 1, fig. D. Type locality: Arrecife, Lanzarote, Canary Islands. HOLOTYPE (by original designation): specimen + 1 radula slide probably of the holotype.

bonosi. *Geitodoris bonosi* Ortea *et* Ballesteros, 1981: 337-341, figs 1-3. Type locality: Cabo Botafoch, Ibiza (Mediterranean Sea). HOLOTYPE (by original designation): specimen.

confusa. *Discodoris confusa* Ballesteros, Llera *et* Ortea, 1984: 236-244, figs 6-8, 10C. Type locality: Las Caletas, Lanzarote, Canary Islands. HOLOTYPE (by original designation): specimen.

edwardsi. *Discodoris edwardsi* Vayssière, 1902: 232-234, pl. 9, figs 4-9. Type locality: *Talisman* (1883) Expedition, off Cape Ghir, Morocco, 2100 m. HOLOTYPE (by monotypy): specimen.

erythraeensis. *Discodoris erythraeensis* Vayssière, 1912: 23, 24, pl. 10, figs 150-152. Type locality: "Nord d'Amboulé", Golfe de Tadjoura, Djibouti. HOLOTYPE (by monotypy, figured by Vayssière 1912, pl. 10, figs 150-152): specimen (dissected), leg. Gravier. **Remarks**: The name *Discodoris erythraeensis* was first introduced by Vayssière (1911) without description (*nomen nudum*).

fava. *Taringa fava* Ballesteros, Llera *et* Ortea, 1984: 246-252, figs 11-14. Type locality: Cubellas, Spain. HOLOTYPE: said to be deposited in MNHN in the original publication, but never presented to the museum.

lutea. *Archidoris maculata* var. *lutea* Vayssière, 1919: 57-65, pl. 4, figs 1-11. Type locality: Carry, Golfe de Marseille, France. SYNTYPES: 2 specimens (dissected). **Remarks:** Thompson & Brown (1984) placed this taxon in the genus *Doris* Linnaeus, 1758, as a synonym of *Doris sticta* (Iredale *et* O'Donoghue, 1923), and therefore it becomes a junior secondary homonym of *Doris lutea* Risso, 1818.

nayarita. *Peltodoris nayarita* Ortea *et* Llera, 1981: 47-51, figs 1-4. Type locality: Isla Isabel, Pacific coast of Mexico. HOLOTYPE (by original designation, figured by Ortea & Llera 1981, figs 1-4): specimen (dissected). **Remarks**: In the original description this species is indistinctly cited as *Peltodoris nayarita* and *Anisodoris nayarita.*

notiperda. *Discodoris notiperda* Risbec, 1956: 15, 16, pl. 9, figs 43-49, pl. 10, figs 50, 51. Type locality: Port Dayot and Nha Trang, Vietnam. SYNTYPES: 9 specimens (3 of them dissected).

oleica. *Taringa oleica* Ortea, Pérez-Sánchez *et* Llera, 1982: 29-33, figs 12-14, pl. 2, fig. E. Type locality: Melenara, Las Palmas, Canary Islands. HOLOTYPE (by original designation): specimen.

perfossa. *Geitodoris perfossa* Ortea, 1990: 109-115, figs 8-11. Type locality: Los Cancajos, La Palma, Canary Islands. HOLOTYPE: said to be deposited in MNHN in the original publication, but never presented to the museum.

rosi. *Discodoris rosi* Ortea, 1979c: 575-579, figs 1-4. Type locality: Oviñana, Asturias, Spain. HOLOTYPE (by original designation): specimen.

rubens. *Discodoris rubens* Vayssière, 1919: 65-67, pl. 6, figs 39-45. Type locality: Carry, Golfe de Marseille, France. SYNTYPES: 3 specimens (dried).

sordida. *Doris sordida* Quoy *et* Gaimard, 1832: 266, pl. 19, figs 12, 13. Type locality: "Îlots aux Cerfs", "Île de France" (= Mauritius), Indian Ocean. SYNTYPE: 1 specimen (dissected), leg. Quoy and Gaimard. **Remarks**: This name is preoccupied by *Doris sordida* Rüppell *et* Leuckart, 1828 (see *sordidata*). Pruvot-Fol (1934b) placed this species in the genus *Discodoris* Bergh, 1877.

sordidata. *Doris sordidata* Abraham, 1877: 206. Type locality: "Îlots aux Cerfs", "Île de France" (= Mauritius), Indian Ocean. SYNTYPE: 1 specimen (dissected), leg. Quoy and Gaimard. **Remarks**: This is a replacement name for *Doris sordida* Quoy *et* Gaimard, 1832, preoccupied by *Doris sordida* Rüppell *et* Leuckart, 1828.

tritorquis. *Taringa tritorquis* Ortea, Pérez-Sánchez *et* Llera, 1982: 38-41, figs 18, 19, pl. 2, fig. G. Type locality: Puerto del Carmen, Lanzarote, Canary Islands. HOLOTYPE (by original designation): specimen.

Family KENTRODORIDIDAE Bergh, 1891

marchadi. *Jorunna marchadi* Risbec, 1956: 16, 17, pl. 11, figs 54-57. Type locality: Pattle Island, Paracels Islands (Southern Sea of China). HOLOTYPE (by monotypy, figured by Risbec, 1956, pl. 11, figs 54-57): specimen (dissected).

onubensis. *Jorunna onubensis* Cervera, García-Gómez *et* García, 1986: 119-128, figs 9-16, pl. 1. Type locality: El Portil, Huelva, Spain. HOLOTYPE (by original designation): specimen (dissected) + radula slide.

Family ASTERONOTIDAE Thiele, 1931

solea. *Doris solea* Cuvier, 1804a: 452-466, pl. 74, figs 1, 2. Type locality: "Île de France" (= Mauritius), Indian Ocean. SYNTYPE (figured by Pruvot-Fol 1934a, pl. 2, figs 1, 2): 1 specimen. **Remarks**: Pruvot-Fol (1934a) placed this species in the genus *Asteronotus* Ehrenberg, 1831.

Family PLATYDORIDIDAE Bergh, 1891

carinata. *Platydoris carinata* Risbec, 1928: 85, 86, fig. 13, pl. 3, fig 10. Type locality: Île Hugon, New Caledonia. SYNTYPES: 2 specimens + spawn.

cruenta. *Doris cruenta* Quoy *et* Gaimard, 1832: 260, 261, pl. 18, figs 5-7. Type locality: New Guinea, Indonesia. SYNTYPE: 1 specimen (dissected). **Remarks**: Pruvot-Fol (1934b) placed this species in the genus *Platydoris* Bergh, 1877.

laminea. *Platydoris laminea* Risbec, 1928: 86, 87, fig. 14, pl. 1, fig. 11. Type locality: New Caledonia. SYNTYPES: 2 specimens.

maculata. *Platydoris maculata* Bouchet, 1977: 37-41, figs 6-8, pl. 2, figs B, C. Type locality: *Thalassa* (1970) Expedition, stn W413, 43°50N - 06°09W, Bay of Biscay, 500-540 m. HOLOTYPE (by original designation): specimen + 1 paratype.

noumeae. *Platydoris noumeae* Risbec, 1928: 80-82, fig. 10, pl. 2, fig. 2. Type locality: New Caledonia. SYNTYPES: 2 specimens.

scabra. *Doris scabra* Cuvier, 1804a: 466. Type locality: Timor, Indonesia. SYNTYPE (figured by Pruvot-Fol 1934a, fig. 3): 1 specimen (dissected), leg. Peron. **Remarks**: Pruvot-Fol (1934b) placed this species in the genus *Platydoris* Bergh, 1877.

spongilla. *Platydoris spongilla* Risbec, 1928: 82-84, fig. 11, pl. 5, fig. 12. Type locality: Rocher à la Voile and Cale de Halage, Nouméa, New Caledonia. SYNTYPE: 1 specimen.

stomascuta. *Platydoris stomascuta* Bouchet, 1977: 35-37, figs 4, 5, pl. 2, fig. D. Type locality: *Biaçores* Expedition, stn 41, 37°43N - 29°04W, off Azores, Prineesse Alice Bank, 450-475 m. HOLOTYPE (by original designation): specimen + 2 paratypes.

Family MIAMIRIDAE Bergh, 1891

rugosa. *Gravieria rugosa* Vayssière, 1912: 30-32, pl. 10, figs 144-149. Type locality: "Îles Musha", Golfe de Tadjoura, Djibouti. HOLOTYPE (by monotypy, figured by Vayssière 1912, pl. 10, figs 144-149): specimen (dissected), leg. Gravier. **Remarks**: The name *Gravieria rugosa* was firstly introduced by Vayssière (1911), without description (*nomen nudum*). This is the type species of the genus *Gravieria* Vayssière, 1912, by monotypy.

Family ALDISIDAE Odhner, 1939

expleta. *Aldisa expleta* Ortea, Pérez-Sánchez *et* Llera, 1982: 10-13, figs 2, 3, pl. 1, fig. A. Type locality: Playa del Carbón, Gran Canaria, Canary Islands. HOLOTYPE (by original designation): specimen. **Remarks**: According to Millen & Gosliner (1985) this species is a junior synonym of *Aldisa banyulensis* Pruvot-Fol, 1951.

nhatrangensis. *Aldisa nhatrangensis* Risbec, 1956: 14, 15, pl. 20, fig. 109, pl. 22, upper right figure. Type locality: Hon Lon, Nha Trang, Vietnam. HOLOTYPE (by original

designation, figured by Risbec 1956, pl. 20, fig. 109, pl. 22): specimen (dissected).

smaragdina. *Aldisa smaragdina* Ortea, Perez-Sanchez *et* Llera, 1982: 14-18, figs 4, 5, pl. 1, fig. B. Type locality: Los Cancajos, La Palma, Canary Islands. HOLOTYPE (by original designation): specimen. **Remarks**: According to Millen & Gosliner (1985) this species is a junior synonym of *Aldisa binotata* Pruvot-Fol, 1953.

Family CHROMODORIDIDAE Bergh, 1892

aeruginosa. *Glossodoris aeruginosa* Rudman, 1995: 12-16, figs 6D, 11-13. Type locality: Banc Gail, between Nouméa and Île Ouen, New Caledonia. HOLOTYPE (by original designation, figured by Rudman 1995, figs 6D, 11-13): specimen (dissected), leg. Laboute.

albofimbria. *Durvilledoris albofimbria* Rudman, 1995: 22-25, figs 6F, 19-21. Type locality: Passe de Koumac, New Caledonia. HOLOTYPE (by original designation, figured by Rudman 1995, figs 6F, 19-21): specimen (dissected).

atromarginata. *Doris atromarginata* Cuvier, 1804a: 473, pl. 74, fig. 6. Type locality: "Mer des Indes" (= Indian Ocean). SYNTYPES: 2 specimens, leg. Péron. **Remarks**: This is the type species of the genus *Doriprismatica* d'Orbigny, 1839, by subsequent designation by Herrmannsen (1846). Following Rudman (1984) *Doriprismatica* is a junior synonym of *Glossodoris* Ehrenberg, 1831.

aureola. *Glossodoris aureola* Rudman, 1995: 16-19, figs 6E, 10B, 14, 15. Type locality: Passe Deverd, off Koumac, New Caledonia. HOLOTYPE (by original designation, figured by Rudman 1995, figs 6E, 10B, 14, 15): specimen (dissected), leg. von Cosel.

boucheti. *Chromodoris boucheti* Rudman, 1982: 190-193, figs 1B, 4, 5. Type locality: northern entrance to Longogoni Passage, Mayotte, Comoro (Indian Ocean). HOLOTYPE (by original designation, figured by Rudman 1982, fig. 1B): specimen + 3 paratypes.

britoi. *Chromodoris britoi* Ortea *et* Pérez-Sánchez, 1983: 62-65, figs 1-3, pl. 1, fig. 3. Type locality: Agua Dulce, Tenerife, Canary Islands. HOLOTYPE (by original designation): specimen.

caledonicum. *Ceratosoma caledonicum* P. Fischer, 1876: 92, 93. Type locality: New Caledonia. SYNTYPES: 2 specimens. **Remarks**: According to Rudman (1988), this is a junior synonym of *Ceratosoma trilobatum* (J. E. Gray, 1827).

cantabrica. *Hypselodoris cantabrica* Bouchet *et* Ortea, 1980: 118-121, figs 1-6, 13. Type locality: Hendaye, France. HOLOTYPE (by original designation): specimen + 11 paratypes.

ciminoi. *Hypselodoris ciminoi* Ortea *et* Valdés *in* Ortea *et al.* 1996: 134-136, figs 12B, 104, 105. Type locality: Bomfin, Angola. HOLOTYPE (by original designation, figured by Ortea *et al.* 1996, figs 12B, 104, 105): specimen (dissected), leg. Rolán.

clavata. *Chromodoris clavata* Risbec, 1928: 151, 152, fig. 42, pl. 7, fig. 2. Type locality: Baie de l'Orphelinat, Nouméa, New Caledonia. SYNTYPE: 1 specimen. **Remarks**: According to Rudman (1982), this is a junior synonym of *Chromodoris striatella* Bergh, 1877.

coi. *Chromodoris coi* Risbec, 1956: 9, 10, pl. 11, figs 58, 59, pl. 22, lower figure. Type locality: Hon Lon, Nha Trang, Vietnam. SYNTYPE: 1 specimen. **Remarks**: Rudman (1987) placed this species in the genus *Chromodoris* Alder *et* Hancock (1855).

decorata. *Chromodoris decorata* Risbec, 1928: 152-154, fig. 43, pl. 7, fig. 4. Type locality: Baie de l'Orphelinat, Nouméa, New Caledonia. SYNTYPE: 1 specimen (dissected). **Remarks**: According to Rudman (1986b), this is a junior synonym of *Hypselodoris maculosa* (Pease, 1871).

dollfusi. *Glossodoris dollfusi* Pruvot-Fol, 1933: 126-128, pl. 1, figs 7, 8, pl. 3, fig. 40. Type locality: Dollfus expedition (29°49'-29°45'N, 32°30'-32°27'E) 31 m, Red Sea, Egypt. HOLOTYPE (by monotypy, figured by Pruvot-Fol 1933, pl. 1, figs 7, 8, pl. 3, fig. 40): specimen (dissected), leg. Dollfus.

elegans. *Doris elegans* Quoy *et* Gaimard, 1832: 273, 274, pl. 20, figs 12-14. Type locality: Tongatapu (Pacific Ocean). SYNTYPE: 1 specimen, leg. Quoy and Gaimard. **Remarks**:

Pruvot-Fol (1934b) placed this species in the genus *Glossodoris* Ehrenberg, 1831.

espinosai. *Hypselodoris espinosai* Ortea *et* Valdés *in* Ortea *et al.* 1996: 139-142, figs 12E, 109-111. Type locality: Puerto Morelos, Quintana Roo, Mexico. HOLOTYPE (by original designation, figured by Ortea *et al.*, 1996, fig. 109): specimen.

flavomarginata. *Hypselodoris flavomarginata* Rudman, 1995: 31-34, figs 6H, 25A, 27-29. Type locality: Grand Coude, Bourail, New Caledonia. HOLOTYPE (by original designation): specimen, leg. Faucompré + 1 paratype.

fontandraui. *Glossodoris fontandraui* Pruvot-Fol, 1951: 24, 25, fig. 11, pl. 1, figs 4, 5, 26. Type locality: Blanes, Spain. NEOTYPE (designated by Ortea *et al.* 1996: 65): specimen. **Remarks:** Ortea *et al.* (1996) placed this species in the genus *Hypselodoris* Stimpson, 1855.

francoesii. *Ceratosoma francoesii* de Rochebrune, 1894: 55. Type locality: Nouméa, New Caledonia. SYNTYPE: 1 specimen, leg. François. **Remarks:** According to Rudman (1988), this is a junior synonym of *Ceratosoma tenue* Abraham, 1876.

francoisae. *Chromodoris francoisae* Bouchet *in* Bouchet & Ortea 1980: 123-125, figs 11, 12, 14. Type locality: "Le Virage", between Ngor and Yof (Senegal). HOLOTYPE (by original designation): specimen + 1 paratype. **Remarks:** Ortea *et al.* (1996) placed this species in the genus *Mexichromis* Bertsch, 1977.

francoisi. *Risbecia francoisi* Odhner, 1934: 248, 249. Type locality: Baie de l'Orphelinat, Nouméa, New Caledonia. SYNTYPE: 1 specimen. **Remarks:** Odhner (1934) established the new genus *Risbecia* with *Ceratosoma francoisi* de Rochebrune, 1894, in the sense of the misidentification of Risbec (1928), as the type species. Under Article 70c (ICZN 1985), with this nomenclatural act Odhner (1934) introduced the new species *Risbecia francoisi* Odhner, 1934, which is the type species of the genus *Risbecia* by original designation. The syntypes of this species are the specimens studied by Risbec (1928).

gasconi. *Hypselodoris gasconi* Ortea *et* Valdés *in* Orrea *et al.* 1996: 120-123, figs 12A, 90-92. Type locality: Calvi, Corsica (Mediterranean Sea). HOLOTYPE (by original designation): specimen.

geometrica. *Chromodoris geometrica* Risbec, 1928: 148-151, fig. 41, pl. 6, fig. 10. Type locality: Anse Vata and Rocher à la Voile, Nouméa, New Caledonia. SYNTYPE: 1 specimen.

gibbosum. *Ceratosoma gibbosum* de Rochebrune, 1894: 55. Type locality: "Dead Joland", Torres Strait, Northern Australia. SYNTYPE: 1 specimen, leg. Lix. **Remarks:** According to Rudman (1988), this is a junior synonym of *Ceratosoma trilobatum* (J. E. Gray, 1827).

gofasi. *Hypselodoris gofasi* Ortea *et* Valdés *in* Ortea *et al.* 1996: 123-129, figs 93-99. Type locality: Santa Maria, Benguela, Angola. HOLOTYPE (by original designation, figured by Ortea *et al.* 1996, fig. 93): specimen, leg. Gofas.

goslineri. *Chromodoris goslineri* Ortea *et* Valdés *in* Ortea *et al.* 1996: 143-146, figs 112-114. Type locality: Villa do Porto, Santa Maria, Azores. HOLOTYPE (by original designation, figured by Ortea *et al.* 1996, fig. 112): specimen (dissected), leg. Gofas.

hikuerensis. *Rosodoris hikuerensis* Pruvot-Fol, 1954: 23-27, fig. 9. Type locality: Hikueru, Tuamotu (Pacific Ocean). HOLOTYPE (by monotypy, figured by Pruvot-Fol 1954, fig. 9): specimen (dissected). **Remarks:** This is the type species of the genus *Rosodoris* Pruvot-Fol, 1954, by original designation. According to Rudman (1986a), *Rosodoris* is a junior synonym of *Glossodoris* Ehrenberg, 1831.

hirsuta. *Cadlinella hirsuta* Rudman, 1995: 2-9, figs 1-5, 6B, 7. Type locality: Baie du Prony, New Caledonia. HOLOTYPE (by original designation): specimen, leg. Laboute + 1 paratype.

jousseaumei. *Ceratosoma jousseaumei* de Rochebrune, 1894: 55. Type locality: Red Sea. SYNTYPES: 2 specimens (1 of them dissected), leg. Botta. **Remarks:** According to Rudman (1988), this is a junior synonym of *Ceratosoma tenue* Abraham, 1876.

koumacensis. *Hypselodoris koumacensis* Rudman, 1995: 34-37, figs 6C, 24B, 30, 31. Type locality: Grande Récif de Koumac, New Caledonia. HOLOTYPE (by original designa-

tion, figured by Rudman 1995, figs 6C, 24B, 30, 31): specimen (dissected).

laboutei. *Noumea laboutei* Rudman, 1986c: 399-401, figs 1H, 15-17. Type locality: Îlot Gi, New Caledonia. HOLOTYPE (by original designation, figured by Rudman 1986c, figs 1H, 15-17): specimen (dissected), leg. Laboute.

lacteola. *Hypselodoris lacteola* Rudman, 1995: 28-30, figs 25B, 26. Type locality: east entrance to Canal Woodin, New Caledonia. HOLOTYPE (by original designation, figured by Rudman 1995, fig. 25B): specimen, leg. Laboute.

lata. *Chromodoris lata* Risbec, 1928: 154-156, fig. 44, pl. 8, fig. 7. Type locality: Île Hugon and Îlot Maître (Nouméa), New Caledonia. SYNTYPES: 4 specimens.

lemniscata. *Doris lemniscata* Quoy *et* Gaimard, 1832: 268, 269, pl. 19, figs 8-11. Type locality: Port Louis, "Île de France" (= Mauritius), Indian Ocean. SYNTYPE: 1 specimen, leg. Quoy and Gaimard (dissected). **Remarks**: This is the type species of the genus *Durvilledoris* Rudman, 1984, by original designation.

lineata. *Doris lineata* Souleyet, 1852: 453, pl. 25, figs 5-9. Type locality: "Îles Sandwich" (= Hawaii). SYNTYPES: 5 specimens, leg. Eydoux and Souleyet. **Remarks**: Eliot (1905) placed this species in the genus *Chromodoris* Alder *et* Hancock, 1855.

lixi. *Ceratosoma lixi* de Rochebrune, 1894: 55. Type locality: "Dead Joland", Torres Strait, Northern Australia. SYNTYPES: 5 specimens, leg. Lix. **Remarks**: According to Rudman (1988), this is a junior synonym of *Ceratosoma trilobatum* (J. E. Gray, 1827).

magnifica. *Doris magnifica* Quoy *et* Gaimard, 1832: 270-272, pl. 20, figs 1-4. Type locality: New Guinea, Indonesia. SYNTYPES: 2 specimens, leg. Quoy and Gaimard. **Remarks**: This is the type species of the genus *Chromodoris* Alder *et* Hancock, 1855, by monotypy.

malacitana. *Hypselodoris malacitana* Luque, 1986: 550-557, figs 42-44. Type locality: La Herradura, Málaga, Spain. NEOTYPE (designated by Ortea *et al.* 1996: 109): specimen.

molloi. *Mexichromis molloi* Ortea *et* Valdés *in* Ortea *et al.* 1996: 152-155, figs 12F, 118-120. Type locality: Isla Picuda, Mochima, Venezuela. HOLOTYPE (by original designation, figured by Ortea *et al.* 1996, figs 12F, 118-120): specimen (dissected).

montrouzieri. *Thorunna montrouzieri* Rudman, 1995: 37-40, figs 6G, 32-34. Type locality: Passe de Koumac, New Caledonia. HOLOTYPE (by original designation, figured by Rudman 1995, figs 6G, 32A, 33, 34): specimen (dissected).

muniaini. *Hypselodoris muniaini* Ortea *et* Valdés *in* Ortea *et al.* 1996: 136-139, figs 106-108. Type locality: Santo Antonio, Príncipe, West Africa. HOLOTYPE (by original designation, figured by Ortea *et al.* 1996, figs 106-108): specimen (dissected), leg. Rolán and Fernandes. **Remarks**: In the header of the original description of this species it is misspelled as *Hypselodoris muniani.*

odhneri. *Risbecia odhneri* Risbec, 1953: 94. Type locality: Baie de l'Orphelinat, Nouméa, New Caledonia. SYNTYPE: 1 specimen. **Remarks**: This species was introduced by Risbec (1953) for the specimens cited by Risbec (1928) under the name "*Ceratosoma francoisi* Rochebrune". These specimens are also the type material of the species *Risbecia francoisi* Odhner, 1934, introduced under Article 70c (ICZN 1985). Therefore, *Risbecia odhneri* and *Risbecia francoisi* are objective synonyms.

ornatissima. *Cadlina ornatissima* Risbec, 1928: 163-165, fig. 47, pl. 8, fig. 4. Type locality: Baie de l'Orphelinat, Nouméa, New Caledonia. HOLOTYPE (by monotypy, figured by Risbec, 1928, fig. 47, pl. 8, fig. 4): specimen (dissected). **Remarks**: This is the type species of the genus *Cadlinella* Thiele, 1931, by monotypy.

orsinii. *Doris orsinii* Verany, 1846: 96, 100, 101. Type locality: Sicily, Italy. NEOTYPE (designated by Ortea *et al.*, 1996: 58): specimen. **Remarks**: Ortea *et al.* (1996) placed this species in the genus *Hypselodoris* Stimpson, 1855.

picta. *Doris picta* Schultz *in* Philippi 1836: 105. Type locality: Catania, Sicily, Italy. NEOTYPE (designated by Ortea *et al.* 1996: 43): specimen. **Remarks**: Ortea *et al.* (1996) placed this species in the genus *Hypselodoris* Stimpson, 1855.

pullata. *Glossodoris pullata* Rudman, 1995: 10-12, figs 6A, 8, 9, 10A. Type locality: Passe

d'Ouraï, near La Foa, New Caledonia. HOLOTYPE (by original designation, figured by Rudman 1995, figs 6A, 8, 9, 10A): specimen (dissected), leg. Faucompré + 1 paratype.

punicea. *Hypselodoris punicea* Rudman, 1995: 25-28, figs 6J, 22-24A. Type locality: Passe de Koumac, New Caledonia. HOLOTYPE (by original designation, figured by Rudman 1995, figs 6J, 22-24A): specimen (dissected).

pustulosa. *Doris pustulosa* Cuvier, 1804a: 452, 473. Type locality: "Mer des Indes" (= Indian Ocean). SYNTYPE (figured by Pruvot-Fol 1934a, fig. 2, pl. 2, figs 3-7): 1 specimen (dissected), leg. Péron. **Remarks**: Pruvot-Fol (1934a) placed this species in the genus *Ceratosoma* J. E. Gray, 1850.

ransoni. *Glossodoris ransoni* Pruvot-Fol, 1954: 18-20, fig. 6. Type locality: Hikueru, Tuamotu (Pacific Ocean). HOLOTYPE (by monotypy): specimen (dissected). **Remarks**: According to Rudman (1987), this is a junior synonym of *Chromodoris kuniei* Pruvot-Fol, 1930.

reticulata. *Doris reticulata* Quoy *et* Gaimard, 1832: 272, 273, pl. 20, figs 9-11. Type locality: Tongatapu (Pacific Ocean). SYNTYPE: 1 specimen, leg. Quoy and Gaimard. **Remarks**: Risbec (1956) placed this species in the genus *Risbecia* Odhner, 1934.

rhopalicum. *Ceratosoma rhopalicum* de Rochebrune, 1894: 55. Type locality: Red Sea. SYNTYPE: 1 specimen, leg. Botta. **Remarks**: According to Rudman (1988), this is a junior synonym of *Ceratosoma tenue* Abraham, 1876.

romeri. *Noumea romeri* Risbec, 1928: 165-167, fig. 48, pl. 5, fig. 5. Type locality: Nouméa, New Caledonia. SYNTYPES: 2 specimens (one of them dissected). **Remarks**: This is the type species of the genus *Noumea* Risbec, 1928, by subsequent designation by Baba (1937).

symmetricus. *Glossodoris symmetricus* Rudman, 1990: 275-279, figs 1C, 6D, 8A, 9D (in part), 10A-D, 11, 12. Type locality: St. Gilles Reef, La Réunion (Indian Ocean). HOLOTYPE (by original designation, figured by Rudman 1990, figs 1C, 6D, 8A, 10B, 11A-F): specimen (dissected), leg. Jay.

tricolor. *Doris tricolor* Cantraine, 1835: 383, 384. Type locality: Accitrezza, Sicily (Mediterranean Sea). NEOTYPE (designated by Ortea *et al.* 1996: 32): specimen. **Remarks**: Ortea *et al.* (1996) placed this species in the genus *Hypselodoris* Stimpson, 1855.

trouilloti. *Chromodoris trouilloti* Risbec, 1928: 146, 147, fig. 39, pl. 8, fig. 5. Type locality: Pointe de l'Artillerie, Nouméa, New Caledonia. SYNTYPES: 2 specimens (dissected).

undulata. *Glossodoris undulata* Pruvot-Fol, 1954: 21-23, fig. 8. Type locality: Hikueru, Tuamotu (Pacific Ocean). SYNTYPES: 3 specimens (dissected). **Remarks**: According to Rudman (1986a), this is a junior synonym of *Glossodoris sibogae* (Bergh, 1905).

verconiforma. *Noumea verconiforma* Rudman, 1995: 19-22, figs 6I, 16-18. Type locality: NW side of Récif de l'Infernet, New Caledonia. HOLOTYPE (by original designation, figured by Rudman 1995, figs 6I, 16-18): specimen (dissected).

versicolor. *Chromodoris versicolor* Risbec, 1928: 147, 148, fig. 40, pl. B, fig. 2, pl. 6, fig. 3. Type locality: Baie de l'Orphelinat, Nouméa, New Caledonia. SYNTYPE: 1 radula. **Remarks**: Risbec (1953) placed this species in the genus *Risbecia* Odhner, 1934.

villafranca. *Doris villafranca* Risso, 1818: 370. Type locality: Blanes, Spain. NEOTYPE (designated by Ortea *et al.* 1996: 22): specimen. **Remarks**: Ortea *et al.* (1996) placed this species in the genus *Hypselodoris* Stimpson, 1855.

xicoi. *Hypselodoris xicoi* Ortea *et* Valdés *in* Ortea *et al.* 1996: 129-133, figs 12C, D, 100-103. Type locality: Esprainha, São Tomé, West Africa. HOLOTYPE (by original designation, figured by Ortea *et al.* 1996, figs 12D, 100B, 101B): specimen, leg. Rolán and Fernandes.

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angolensis. *Dendrodoris angolensis* Valdés *et* Ortea *in* Valdés *et al.* 1996: 20-23, figs 2F, 11, 12C. Type locality: Luanda, Angola. HOLOTYPE (by original designation): specimen, leg. Gofas + 2 paratypes.

aurea. *Doris aurea* Quoy *et* Gaimard, 1832: 265, pl. 19, figs 4-7. Type locality: Jervis Bay, Australia. SYNTYPES: 5 specimens (2 of

them dissected). **Remarks**: Pruvot-Fol (1934b) placed this species in the genus *Dendrodoris* Ehrenberg, 1831.

communis. *Doridopsis communis* Risbec, 1928: 67-69, fig. 7, pl. A, fig. 2, pl. 1, fig. 6. Type locality: Pointe de l'Artillerie, Nouméa, New Caledonia. SYNTYPES: 2 specimens. **Remarks**: According to Brodie *et al.* (1997), this is a junior synonym of *Dendrodoris fumata* (Rüppell *et* Leuckart, 1828).

fosseti. *Doridopsis fosseti* Risbec, 1928: 64, 65, pl. 5, fig. 4. Type locality: Pointe de l'Artillerie, Nouméa, New Caledonia. SYNTYPE (figured by Risbec 1928, pl. 5, fig. 4): 1 specimen.

grandiflora. *Doris grandiflora* Rapp, 1827: 520, 521, fig. 3. Type locality: Strait of Gibraltar, 36°09'N - 06°09'W, Spain. NEOTYPE (designated by Valdés *et al.* 1996: 9): specimen. **Remarks**: *Doris grandiflora* has been placed in the Official List of Specific Names in Zoology, Opinion 1805 (ICZN 1995). Valdés *et al.* (1996) placed this species in the genus *Dendrodoris* Ehrenberg, 1831.

herytra. *Dendrodoris herytra* Valdés *et* Ortea *in* Valdés *et al.* 1996: 25-27, figs 2G, H, 12B, 14. Type locality: Madeira. HOLOTYPE (by original designation): specimen, leg. Wirtz.

limbata. *Doris limbata* Cuvier, 1804a: 468, 469, pl. 74, fig. 3. Type locality: Marseille, France. NEOTYPE (designated by Valdés *et al.* 1996: 5): specimen. **Remarks**: Valdés *et al.* (1996) placed this species in the genus *Dendrodoris* Ehrenberg, 1831.

minima. *Dendrodoris minima* Pruvot-Fol, 1951: 47. Type locality: Muros de Nalón, Asturias, Spain. NEOTYPE (designated by Valdés & Ortea 1997: 249): specimen, leg. Rodríguez. **Remarks**: Valdés & Ortea (1997) designated the same specimen as neotype of *Doriopsilla pelseneeri* d'Oliveira, 1895, and therefore both names become objective synonyms.

mollis. *Doridopsis mollis* Risbec, 1928: 65, 66, fig. 6, pl. 2, fig. 4. Type locality: New Caledonia. SYNTYPES: 2 specimens. **Remarks**: According to Brodie *et al.* (1997), this is a junior synonym of *Dendrodoris nigra* (Stimpson, 1855).

nigropunctata. *Doriopsis nigropunctata* Vayssière, 1912: 77, 78, pl. 7, fig. 109. Type locality: Djibouti. HOLOTYPE (by monotypy, figured by Vayssière 1912, pl. 7, fig. 109): specimen (dissected), leg. Gravier. **Remarks**: This species probably must be placed in the genus *Dendrodoris* Ehrenberg, 1831.

pelseneeri. *Doriopsilla pelseneeri* d'Oliveira, 1895: 12, 13. Type locality: Muros de Nalón, Spain. NEOTYPE (designated by Valdés & Ortea 1997: 249): specimen, leg. Rodríguez.

punctata. *Doris punctata* Quoy *et* Gaimard, 1832: 262, pl. 18, figs 8-10. Type locality: "Le Havre Carteret", New Ireland, Bismarck Archipelago. SYNTYPE: 1 specimen, leg. Quoy and Gaimard. **Remarks**: This name is preoccupied by *Doris punctata* Rüppell *et* Leuckart, 1828 (see *rufopunctata*). Pruvot-Fol (1934b) placed this species in the genus *Dendrodoris* Ehrenberg, 1831.

racemosa. *Dendrodoris racemosa* Pruvot-Fol, 1951: 47. Type locality: Muros de Nalón, Spain. NEOTYPE (designated by Valdés & Ortea 1997: 249): specimen, leg. Rodríguez. **Remarks**: Valdés & Ortea (1997) designated the same specimen as neotype of *Doriopsilla pelseneeri* d'Oliveira, 1895, and therefore both names become objective synonyms.

rosea. *Doriopsis rosea* Vayssière, 1912: 82, 83, pl. 1, fig. 2, pl. 10, fig. 153. Type locality: near Obock, Golfe de Tadjoura, Djibouti. SYNTYPES (one figured by Vayssière 1912, pl 1, fig. 2, pl. 10, fig. 153): 1 specimen (dissected), leg. Jousseaume; 1 specimen (dissected) leg. Gravier. **Remarks**: The name *Doriopsis rosea* was firstly introduced by Vayssière (1911) without description (*nomen nudum*). According to Brodie *et al.* (1997), this is a junior synonym of *Dendrodoris fumata* (Rüppell *et* Leuckart, 1828).

rufopunctata. *Dendrodoris rufopunctata* Pruvot-Fol, 1934b: 60, 61. Type locality: "Le Havre Carteret", New Ireland, Bismarck Archipelago. SYNTYPE: 1 specimen, leg. Quoy and Gaimard. **Remarks**: This is a replacement name for *Doris punctata* Quoy *et* Gaimard, 1832, preoccupied by *Doris punctata* Rüppell *et* Leuckart, 1828.

senegalensis. *Dendrodoris senegalensis* Bouchet, 1975a: 124-127, figs 3, 4, pl. 1, fig. 2. Type locality: "Le Virage" between Ngor and Yof,

Cap Vert Peninsula, Senegal. HOLOTYPE (by original designation): specimen + 2 paratypes. **Remarks**: Bouchet (1975a), originally designated a "Lectotype" for this species. However, following Article 73a (i) (ICZN 1985), if an author when establishing a new nominal species states that one specimen is "the type", or uses some equivalent expression, that specimen is the holotype by original designation.

tuberculosa. *Doris tuberculosa* Quoy *et* Gaimard, 1832: 248, 249, pl. 16, figs 1, 2. Type locality: "Port Dorey" (= Manokwari), Irian Jaya, Indonesia. SYNTYPE: 1 specimen (dissected). **Remarks**: Pruvot-Fol (1934b) placed this species in the genus *Dendrodoris* Ehrenberg, 1831.

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albonigra. *Phyllidia albonigra* Quoy *et* Gaimard, 1832: 291, 292, pl. 21, figs 26, 27. Type locality: Tongatapu (Pacific Ocean). LECTOTYPE (selected by Brunckhorst 1993, figured by Quoy & Gaimard 1832, pl. 21, figs 26, 27): specimen. **Remarks**: According to Brunckhorst (1993), this is a junior synonym of *Phyllidiella pustulosa* (Cuvier, 1804).

aurata. *Phyllidia aurata* Pruvot-Fol, 1952: 408-411, figs 1-9. Type locality: Cannes, France. HOLOTYPE (by monotypy, figured by Pruvot-Fol 1952, figs 1-9): specimen (dissected). **Remarks**: According to Brunckhorst & Willan (1989), this is a junior synonym of *Phyllidia flava* Aradas, 1847.

bayi. *Fryeria bayi* Bouchet, 1983: 65-68, figs 1, 2. Type locality: Punta Bianca, Corsica (Mediterranean Sea). HOLOTYPE (by original designation, figured by Bouchet 1983, fig. 1): specimen + 1 paratype.

berghi. *Phyllidiopsis berghi* Vayssière, 1902: 237-242, pl. 9, figs 10-16, pl. 10, fig. 17. Type locality: *Talisman* (1883) Expedition, stn 141, 45°59.00'N - 04°09.46'W, Bay of Biscay, 1480 m. HOLOTYPE (by monotypy, figured by Vayssière 1902, pls 9, 10 and Valdés & Ortea 1996, fig. 1B): specimen (dissected).

borbonica. *Phyllidia borbonica* unavailable. **Remarks**: Brunckhorst (1993) studied one specimen deposited in MNHN labelled "*Phyllidia borbonica* Cuv.", and pointed out that it is a large specimen of *P. varicosa*. At the same time, he indicated that the species *Phyllidia borbonica* was introduced by Cuvier (1804c), and listed this name in the synonymy of *P. varicosa*. However, in that paper Cuvier did not introduce any new species, but just remarked that he was the first author who described the genus *Phyllidia* based on a single specimen collected from "Île Bourbon" (= La Réunion). Therefore, Brunckhorst (1993) is the first author who introduced the manuscript name *P. borbonica*, but in synonymy, so that it is unavailable (ICZN 1985, Article 11e). For additional information on this specimen see also the remarks on *Phyllidia trilineata* Cuvier, 1804 and *Phyllidia varicosa* Lamarck, 1801.

boucheti. *Phyllidiopsis boucheti* Valdés *et* Ortea, 1996: 5, 6, figs 1D, 5 (in part), 6. Type locality: Punta de la Rasca, Tenerife, Canary Islands. HOLOTYPE (by original designation, figured by Valdés & Ortea 1996, fig. 1D): specimen + 1 paratype.

catena. *Phyllidia catena* Pruvot-Fol, 1956b: 70-72, figs 6, 7. Type locality: Mayotte and Mauritius (Indian Ocean). SYNTYPES [one figured by Pruvot-Fol 1956b, figs 6 (in part), 7]: 2 specimens, leg. Mathieu; 1 specimen (dissected), leg. Cloué. **Remarks**: According to Brunckhorst (1993), this is a junior synonym of *Phyllidiella zeylanica* (Kelaart, 1859).

dautzenbergi. *Phyllidia dautzenbergi* Vayssière, 1912: 85-87, pl. 1, figs 14, 15. Type locality: "Nord d'Ambouli", Golfe de Tadjoura, Djibouti. HOLOTYPE (by monotypy, figured by Vayssière 1912, pl. 1, figs 14, 15): specimen, leg. Gravier. **Remarks**: The name *Phyllidia dautzenbergi* was firstly introduced by Vayssière (1911) without description (*nomen nudum*). Brunckhorst (1993) placed this species in the genus *Phyllidiopsis* Bergh, 1875.

flava. *Phyllidia flava* Aradas, 1847: 121. Type locality: Xlendi, Gozo, Malta. NEOTYPE (designated by Brunckhorst & Willan 1989: 209, figured by Brunckhorst & Willan 1989, fig. 1): specimen + photo.

gofasi. *Reticulidia gofasi* Valdés *et* Ortea, 1996: 7, 8, figs 1F, 4C, 5 (in part), 8. Type locality: *Seamount 1* Expedition, stn DW61,

36°40.02'N - 14°16.00'W, Josephine Bank, North Eastern Atlantic, 200-205 m. HOLOTYPE (by original designation, figured by Valdés & Ortea 1996, fig. 1F): specimen + 2 paratypes.

gynenopla. *Phyllidiopsis gynenopla* Bouchet, 1977: 50-53, figs 18, 19, pl. 2, fig. E. Type locality: *Biaçores* Expedition, stn 159, 37°26'N - 25°51'W, off Santa Maria, Azores, 525-600 m. HOLOTYPE (by original designation, figured by Bouchet 1977, figs 18, 19, pl. 2, fig. E and Valdés & Ortea 1996, fig. 1C): specimen (dissected). **Remarks**: According to Valdés & Ortea (1996), this is a junior synonym of *Phyllidiopsis berghi* Vayssière, 1902.

honloni. *Phyllidia honloni* Risbec, 1956: 22, 23, pl. 14, figs 71-75, pl. 15, figs 79-81. Type locality: Hon Lon, Nha Trang, Vietnam. LECTOTYPE (selected by Brunckhorst, 1993): specimen + 3 paralectotypes. **Remarks**: According to Brunckhorst (1993), this is a junior synonym of *Phyllidia varicosa* Lamarck, 1801.

krempfi. *Phyllidiopsis krempfi* Pruvot-Fol, 1957: 120, 121, figs 41-49, pl. 1, figs 7, 8. Type locality: Nha Trang, Vietnam. HOLOTYPE (by monotypy, figured by Pruvot-Fol 1957, figs 41-49, pl. 1, figs 7, 8): specimen.

nigra. *Phyllidia nigra* van Hasselt, 1824: 244. Type locality: Cu Lao Hon "Île Poulo Cecir de Mer", Vietnam. NEOTYPE (designated by Brunckhorst, 1993: 55): specimen. **Remarks**: Brunckhorst (1993) placed this species in the genus *Phyllidiella* Bergh, 1869.

ocellata. *Phyllidia ocellata* Cuvier, 1804b: 269, pl. 18, fig. 7. Type locality: Timor, Indonesia. LECTOTYPE (selected by Brunckhorst 1993, figured by Pruvot-Fol 1956b, fig. 2): specimen (dissected), leg. Péron and Lesueur.

pulitzeri. *Phyllidia pulitzeri* Pruvot-Fol, 1963: 566-569, figs 1-6, pl. 1. Type locality: Portofino, Genova, Italy. HOLOTYPE (by original designation, figured by Pruvot-Fol 1963, figs 1-6, pl. 1): specimen, leg. Pulitzer. NEOTYPE (designated by Wägele, 1985: 65, figured by Brunckhorst & Willan 1989, fig. 1): specimen + photo from Xlendi, Gozo, Malta. **Remarks**: Wägele (1985) designated a neotype of this species because at that time the holotype was considered lost. Later, Brunckhorst & Willan (1989) selected the same specimen as neotype of *Phyllidia flava* Aradas, 1847, to fix the synonymy between both nominal species. However, we have rediscovered the holotype of *Phyllidia pulitzeri* in MNHN, and therefore this case should be submitted to the Commission (ICZN 1985: Article 75h).

pustulosa. *Phyllidia pustulosa* Cuvier, 1804b: 268, pl. 18, fig. 8, Type locality: Timor, Indonesia. LECTOTYPE (selected by Brunckhorst 1993, figured by Cuvier 1804b, pl. A, fig. 8 and Brunckhorst 1993, fig. 27A): specimen, leg. Péron and Lesueur. **Remarks**: This is the type species of the genus *Phyllidiella* Bergh, 1869, by subsequent designation by Brunckhorst (1993).

serenei. *Phyllidia serenei* Risbec, 1956: 24, 25, pl. 16, figs 82-84, pl. 17, figs 86-89. Type locality: "Île Poulo Cecir de Mer" (= Cu Lao Hon), Vietnam. LECTOTYPE (selected by Brunckhorst, 1993): specimen + 3 paralectotypes. **Remarks**: Brunckhorst (1993) designated the lectotype of *Phyllidia serenei* as neotype of *Phyllidiella nigra* (van Hasselt, 1824), and therefore both names become objective synonyms.

trilineata. *Phyllidia trilineata* Cuvier, 1804b: 268, pl. 18, figs 1-6. Type locality: La Réunion, Indian Ocean. SYNTYPE (figured by Cuvier 1804b, pl. 18, figs 1-4): 1 specimen (dissected) (Fig. 10B). NEOTYPE (designated by Brunckhorst 1993: 27, figured by Brunckhorst 1993, fig. 23): specimen, leg. Drivas and Jay. **Remarks**: Cuvier (1797) established the generic name *Phyllidia* for a single specimen collected from "Île Bourbon" (= La Réunion), but did not name the species. Lamarck (1801) erected the specific name *Phyllidia varicosa* for the specimen seen by Cuvier (1797). Cuvier (1804b) commented that the species on which he himself based the genus *Phyllidia* must be named *Phyllidia trilineata* instead of *P. varicosa* because the former name is more appropriate. At the same time, he described and figured *P. trilineata* based on the original specimen (from La Réunion) and two additional individuals (considerably smaller in size) collected by Péron from "Mer des Indes". The examination of the specimen





Fig. 10. — **A**, Holotype of *Phyllidia varicosa* and syntype of *Phyllidia trilineata*, 60.4 mm; **B**, Photocopy of Cuvier's (1804b, pl. 18, fig. 1) drawing of *Phyllidia trilineata*.

which Brunckhorst considered the holotype of the unavailable species *P. borbonica* (see remarks on *Phyllidia borbonica*) reveals that it is one of the syntypes of *P. trilineata* figured by Cuvier (1804b, pl. 18, figs 1-4), see Figs 10A, B. As remarked above, this specimen is labelled "*Phyllidia borbonica* Cuv.", which unequivocally indicates that it was collected from La Réunion. In addition, this specimen is very large, so evidently it is the specimen on which Cuvier (1797) based the genus *Phyllidia* (the specimens collected later were considerably smaller), and therefore the holotype of *P. varicosa*. In the ancient catalogue of specimens in alcohol of MNHN this specimen is registered within the types of *Phyllidia ocellata* Cuvier, 1804 and *Phyllidia pustulosa* Cuvier, 1804, both collected from Timor by Péron and Lessueur. The other syntypes of *P. trilineata* are not registered and it is probable that they have never been deposited in MNHN collections. Brunckhorst (1993) selected a neotype for *P. varicosa* and *P. trilineata*, but since the original type material of this species has been rediscovered, this case must be submitted to the Commission (ICZN 1985: Article 75h).

tuberculata. *Phyllidia tuberculata* Risbec, 1928: 59, 60, fig. 3, pl. A, fig. 1, pl. 1, fig. 2. Type locality: Baie de l'Orphelinat, Nouméa, New Caledonia. SYNTYPE: 1 specimen (dissected). **Remarks**: According to Brunckhorst (1993), this is a junior synonym of *Phyllidiopsis cardinalis* Bergh, 1875.

varicosa. *Phyllidia varicosa* Lamarck, 1801: 66. Type locality: La Réunion, Indian Ocean. HOLOTYPE (by monotypy, figured by Cuvier 1804b, pl. 18, figs 1-4): specimen (dissected) (Fig. 10A). NEOTYPE (designated by Brunckhorst 1993: 27, figured by Brunckhorst 1993, fig. 23): specimen, leg. Drivas and Jay. **Remarks**: As indicated above (see remarks on *Phyllidia borbonica* and *Phyllidia trilineata*), the syntype of *P. trilineata* figured by Cuvier (1804b, pl. 18, figs 1-4), is actually in MNHN collections. This specimen labelled "*Phyllidia borbonica* Cuv." is the holotype by monotypy of *P. varicosa*. Brunckhorst (1993) selected a neotype for *P. varicosa* and *P. trilineata*, but since the original type material has been rediscovered, this case must be submitted to the Commission (ICZN 1985: Article 75h).

Incertae sedis

alboranica. *Doris (?) alboranica* Bouchet, 1977: 29-34, figs 1, 2. Type locality: *Polymède 2* Expedition, stn 66, 36°05N - 4°52W, Alboran Sea, 910 m. HOLOTYPE (by original designation, figured by Bouchet 1977, figs 1, 2): specimen (dissected).

rigida. *Spongiodoris rigida* Pruvot-Fol, 1933: 131-133, pl. 2, figs 12-17. Type locality: Gulf of Suez, Egypt. SYNTYPE: 1 specimen, leg. Dollfus. **Remarks**: This is the type species of the genus *Spongiodoris* Pruvot-Fol, 1933, by monotypy.

NUDIBRANCHIA-DENDRONOTINA

Family Tritoniidae Lamarck, 1809

episcopalis. *Tritonia episcopalis* Bouchet, 1977:

55-57, figs 22, 23, pl. 1, figs E, F, pl. 3, figs C, D. Type locality: *Thalassa* (1973) Expedition, stn Z409, 47°43N - 8°04W, off Brittany, France, 1035-1080 m. HOLOTYPE (by original designation): specimen + 2 paratypes.

gravieri. *Tritoniopsis gravieri* Vayssière, 1912: 90-95, pl. 6, figs 78-86. Type locality: Golfe de Tadjoura, Djibouti. HOLOTYPE (by monotypy, figured by Vayssière 1912, pl. 6, figs 78-86): specimen (dissected), leg. Gravier. **Remarks**: The name *Tritoniopsis gravieri* was firstly introduced by Vayssière (1911) without description (*nomen nudum*).

hombergii. *Tritonia hombergii* Cuvier, 1802: 483-494, pls 1, 2. Type locality: Le Havre, France. SYNTYPES: 3 specimens, leg. Homberg. **Remarks**: This is the type species of the genus *Tritonia* Cuvier, 1797, by designation under plenary powers, Opinion 668 (ICZN 1963).

poirieri. *Microlophus poirieri* Mabille *et* de Rochebrune *in* de Rochebrune & Mabille 1889: 11, 12, pl. 6, fig. 1. Type locality: "Baie Orange", Punta Atenas, Chile. SYNTYPE: 1 specimen. **Remarks**: This is the type species of *Microlophus* Mabille *et* de Rochebrune, 1889, by monotypy.

Family DOTIDAE J. E. Gray, 1853

arteoi. *Doto arteoi* Ortea, 1978: 389-392, figs A-D. Type locality: Concha de Artedo, Asturias, Spain. HOLOTYPE (by original designation): specimen.

cervicenigra. *Doto cervicenigra* Ortea *et* Bouchet, 1989: 265, 266, figs 5-7, 9. Type locality: La Revellata, Calvi, Corsica (Mediterranean Sea). HOLOTYPE (by original designation, figured by Ortea & Bouchet 1989, figs 5-7, 9): specimen.

cindyneutes. *Doto cindyneutes* Bouchet, 1977: 57, 58, fig. 24. Type locality: *Thalassa* (1973) Expedition, stn Z435, 48°40N - 09°53W, off Brittany, France, 1050 m. HOLOTYPE (by original designation): specimen + 1 paratype.

fluctifraga. *Doto fluctifraga* Ortea *et* Pérez-Sánchez, 1982: 79-83, figs 1-4. Type locality: La Garita, Gran Canaria, Canary Islands. HOLOTYPE (by original designation): specimen.

fragaria. *Doto fragaria* Ortea *et* Bouchet, 1989: 262-264, figs 1-4, 8. Type locality: near La Revellata, Calvi, Corsica (Mediterranean Sea). HOLOTYPE (by original designation, figured by Ortea & Bouchet 1989, figs 2, 3, 8): specimen + spawn + prey.

furva. *Doto furva* García-Gómez *et* Ortea, 1984: 208-211, figs 1, 2, pl. 1, fig. A. Type locality: Tatifa, Spain. HOLOTYPE (by original designation): specimen.

racemosa. *Doto racemosa* Risbec, 1928: 269, 270, fig. 90, pl. 11, fig. 3. Type locality: Rocher à la Voile, Nouméa, New Caledonia. SYNTYPE: 1 specimen.

ussi. *Doto ussi* Ortea, 1982b: 1-6, figs 1-3. Type locality: Mayotte, Comoros (Indian Ocean). HOLOTYPE (by original designation): specimen + photo + 1 paratype.

Family SCYLLAEIDAE Alder *et* Hancock, 1855

rosea. *Melibe rosea* Rang, 1829a: 130, pl. 3, fig. 3. Type locality: Cape of Good Hope, Southern Africa. SYNTYPE: 1 specimen, leg. Rang.

NUDIBRANCHIA-ARMININA

Family ARMINIDAE Iredale *et* O'Donoghue, 1923

digueti. *Armina digueti* Pruvot-Fol, 1955: 464-466, figs 8-10. Type locality: Baja California, Mexico. HOLOTYPE (by original designation, figured by Pruvot-Fol 1955, figs 8-10): specimen (dissected), leg. Diguet.

Family ZEPHYRINIDAE Iredale *et* O'Donoghue, 1923

praeclara. *Antiopella praeclara* Bouchet, 1975a: 127-130, fig. 5, pl. 1, fig. 3. Type locality: Île aux Serpents, near Dakar, Senegal. HOLOTYPE (by original designation): specimen + 2 paratypes. **Remarks**: Bouchet (1975a) originally designated a 25 mm long specimen the "Lectotype" for this species. However, following the Article 73a (i) (ICZN 1985), if an author when establishing a new nominal spe-

cies states that one specimen is "the type", or uses some equivalent expression, that specimen is the holotype by original designation.

NUDIBRANCHIA-AEOLIDINA

Family FLABELLINIDAE Bergh, 1889

baetica. *Flabellina baetica* García-Gómez, 1984: 61-64, pls 1, 2A. Type locality: Tarifa, Spain. HOLOTYPE (by original designation): specimen.

barentsi. *Coryphella barentsi* Vayssière, 1913: 2-5, figs 1-6. Type locality: mouth of river Rogacheva, Belush'ya Guba Bay, SW coast of Novaya Zemlya, Russia. HOLOTYPE (by monotypy, figured by Vayssière 1913, figs 1-6): specimen (dissected).

Family EUBRANCHIDAE Odhner, 1934

arci. *Eubranchus arci* Ortea, 1980: 170-174, figs 1, 2. Type locality: Punta Hidalgo, Tenerife, Canary Islands. HOLOTYPE (by original designation): specimen.

linensis. *Eubranchus linensis* García-Gómez, Cervera *et* García, 1990: 585-591, figs 1-6, 11. Type locality: Tarifa, Spain. HOLOTYPE (by original designation): specimen (dissected).

prietoi. *Eubranchus prietoi* Llera *et* Ortea, 1981: 266-270, figs 1-3, pl. 1. Type locality: Verdicio, Asturias, Spain. HOLOTYPE (by original designation, figured by Llera & Ortea 1981, pl. 1, figs D, E): specimen.

Family AEOLIDIIDAE Gray, 1827

annulata. *Eolidia annulata* Quoy *et* Gaimard, 1832: 287, 288, pl. 21, figs 15-18. Type locality: "Port Dorey" (= Manokwari), Irian Jaya, Indonesia. SYNTYPE (figured by Quoy & Gaimard 1833, pl. 21, figs 15-18): 1 specimen. **Remarks**: Pruvot-Fol (1934b) placed this species in the genus *Cerberilla* Bergh, 1873.

cryoporos. *Baeolidia cryoporos* Bouchet, 1977: 60-63, figs 26, 27. Type locality: *Biogas III* Expedition, stn CV24, 47°33'N - 08°34'W, Bay of Biscay, 2110 m. HOLOTYPE (by original designation, figured by Bouchet 1977, figs 26, 27): specimen (dissected).

paradoxa. *Eolidina paradoxa* Quatrefages, 1843: 31. Type locality: Saint-Vaast, France. SYNTYPE: 1 specimen.

quoyi. *Baeolidia quoyi* Pruvot-Fol, 1934b: 56, fig. 19. Type locality: unknown. HOLOTYPE (by monotypy): specimen (dissected), leg. Quoy and Gaimard.

ransoni. *Aeolidiopsis ransoni* Pruvot-Fol, 1956a: 228-231, figs 1-11. Type locality: Île Kaukura, Tuamotu (Pacific Ocean). SYNTYPE: 1 specimen (dissected), leg. Ranson. **Remarks**: This is the type species of the genus *Aeolidiopsis* Pruvot-Fol, 1956, by original designation.

Family GLAUCIDAE J. E. Gray, 1827

alba. *Algarvia alba* García-Gómez *et* Cervera, 1990: 734-740, figs 1-9. Type locality: Baia da Baleeira, Sagres, Portugal. HOLOTYPE (by original designation): specimen. **Remarks**: This is the type species of the genus *Algarvia* García-Gómez *et* Cervera, 1989, by original designation.

anadoni. *Rioselleolis anadoni* Ortea, 1979a: 132-138, pls 1-3. Type locality: Ribadesella, Asturias, Spain. HOLOTYPE (by original designation): specimen. **Remarks**: This is the type species of the genus *Rioselleolis* Ortea, 1979, by original designation, considered by Rolán *et al.* (1991) as a junior synonym of *Babakina* Roller, 1973.

bouraílli. *Aeolidia bouraílli* Risbec, 1928: 254-256, fig. 83, pl. 9, fig. 2. Type locality: Île Nou (Nouméa) and Bourail, New Caledonia. SYNTYPE: 1 specimen. **Remarks**: Rudman (1980) placed this species in the genus *Phidiana* J. E. Gray, 1850.

cornuta. *Aeolidia cornuta* Risbec, 1928: 235, 236, fig. 71, pl. 11, fig. 5. Type locality: Pointe de l'Artillerie (Nouméa) and Bourail, New Caledonia. SYNTYPES: 3 specimens.

dangeri. *Aeolidia dangeri* Risbec, 1928: 252-254, fig. 82, pl. 9, fig. 1. Type locality: Rocher à la Voile, Nouméa, New Caledonia. SYNTYPE: 1 specimen.

diffusa. *Aeolidia diffusa* Risbec, 1928: 242-244, fig. 75, pl. D, fig. 2, pl. 12, fig. 2. Type locali-

ty: New Caledonia. SYNTYPE: 1 specimen.

ducrosi. *Aeolidia ducrosi* Risbec, 1928: 232, 233, fig. 69, pl. 11, fig. 7. Type locality: Rocher à la Voile, Nouméa, New Caledonia. SYNTYPE: 1 specimen.

joubini. *Aeolidia joubini* Risbec, 1928: 233-235, fig. 70, pl. 10, fig. 2. Type locality: Nouméa, New Caledonia. SYNTYPE: 1 specimen.

poindimiei. *Aeolidia poindimiei* Risbec, 1928: 246, 247, fig. 78, pl. 9, fig. 3. Type locality: Poindimié and Île N'Du Kué, New Caledonia. SYNTYPE: 1 specimen. **Remarks**: Rudman (1991) placed this species in the genus *Phyllodesmium* Ehrenberg, 1831.

trunca. *Aeolidia trunca* Risbec, 1928: 236-238, fig. 72, pl. 9, fig. 8. Type locality: Rocher à la Voile and Pointe de l'Artillerie, Nouméa, New Caledonia. SYNTYPE: 1 specimen.

violacea. *Aeolidia violacea* Risbec, 1928: 251, 252, fig. 81, pl. 11, fig. 2. Type locality: Île Nou and Rocher à la Voile, Nouméa, New Caledonia. SYNTYPE: 1 specimen.

vitreus. *Favorinus vitreus* Ortea, 1982c: 45-48, figs 1, 2. Type locality: Los Cristianos, Tenerife, Canary Islands. HOLOTYPE (by original designation): specimen + photo.

Family TERGIPEDIDAE Bergh, 1889

francaisi. *Guyvalvoria francaisi* Vayssière, 1906a: 147. Type locality: "Île Wändel" (= Renaud Island), Antarctica. HOLOTYPE (by monotypy): specimen (dissected). **Remarks**: This is the type species of the genus *Guyvalvoria* Vayssière, 1906, by monotypy.

Family FIONIDAE J. E. Gray, 1857

longicauda. *Eolidia longicauda* Quoy et Gaimard, 1832: 288-290, pl. 21, figs 19, 20. Type locality: Cook Strait, New Zealand. SYNTYPES: 6 specimens. **Remarks**: This is the type species of the genus *Dolicheolis* Finlay, 1926, by monotypy.

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INDEX

Index of names including family and higher category taxa.
Page number in italics refer to illustrations.

ABBREVIATIONS

Aeo	Aeolidina,
Arm	Armina,
Aply	Aplysiomorpha,
Ceph	Cephalaspidea,
Den	Dendronotina,
Dor	Doridina,
Nudi	Nudibranchia,
Nota	Notaspidea,
Saco	Sacoglossa,
Thec	Thecosomata.

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